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Charles E. Johnson
SUNY College of Environmental Science and Forestry

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OF

THE NEW YORK STATE COLLEGE OF FORESTRY
AT SYRACUSE UNIVERSITY
SAMUEL N. SPRING, *Dean*

Roosevelt Wild Life Annals

VOLUME 3 NUMBERS 3 AND 4

OF THE

Roosevelt Wild Life Forest Experiment Station

PARASITES OF ONEIDA LAKE FISHES

PART 3. *A Biological and Ecological Survey of the Worm Parasites*

PART 4. *Additional Notes on Parasites of Oneida Lake Fishes, including descriptions of new species*

CONTENTS OF RECENT ROOSEVELT WILD LIFE BULLETINS AND ANNALS

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PARASITES OF ONEIDA LAKE FISHES

PART III. A BIOLOGICAL AND ECOLOGICAL SURVEY OF THE WORM PARASITES

By Harley J. Van Cleave * and Justus F. Mueller **

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SECTION 1. INTRODUCTION

General Considerations.—In the program of the Roosevelt Wild Life Forest Experiment Station, there have been a number of investigations centering around the general topic of the biology of the Oneida Lake region. Two of these dealt in introductory manner with the animal parasites of the vertebrates of Oneida Lake. A report by Pratt (1923) covered the general field of animal parasites in cursory manner and one by Van Cleave (1923) was confined to the Acanthocephala.

During the year 1928, the junior author began investigations of the worm parasites of vertebrates of the Oneida Lake region. In the summer of 1929, the senior author became associated in this program and subsequently the field work was carried on jointly through the summers of 1929 to 1931 inclusive.

Parts I and II of this survey have already been published (Van Cleave and Mueller, 1932; Mueller and Van Cleave, 1932). These earlier publications were prefatory to the final report and disposed of the relatively large number of previously unknown species encountered in the course of the survey. The relations between fishes and their parasites and correlations which may exist between habitat and degree of infestation are problems on which little information has been available. The present study is presented as a contribution toward the understanding of these problems. Both authors have contributed equally in the study of material and in the composition of the manuscript.

During the four years covered by this investigation, many persons have rendered assistance to the writers. Dr. C. E. Johnson, Director of the Roosevelt Station, was responsible for initiating the study. Assistant Director W. A. Dence has given aid in the identification of fish hosts and in the preparation of the manuscripts. Many of the local fishermen have given advice and assistance generously, among whom we may especially mention Mr. Harry Best, Mr. R. Landgraff and Mr. J. Dawley, of Cleveland, New York, and Mr. Fred M. Theisen of Brewerton, New York. During the summer of 1931, Mr. Richard Klix, of Cleveland, New York, became a field assistant in charge of our fishing operations. The list of professional colleagues who have loaned specimens of parasites for comparative study and in other ways given assistance in the technical aspects of the research has been extensive. To all these colleagues general indebtedness is here admitted and specific acknowledgment is made in the text in connection with the treatment of the genera and species of parasites concerned. We are especially indebted to Mr. S. H. Hopkins, of the University of Illinois, who read the manuscript on the family Allocreadiidae and gave valued suggestions.

An examination of more than twelve hundred individual fish representing thirty-four species has given specific information on the occurrence and correlations of more than ninety species of worm parasites in Oneida Lake fishes. Seasonal variations affecting the host are among the most significant factors influencing relative numbers of parasites. The studies of Van Cleave (1916), of Pearse (1924) and of Holl (1932) show characteristic instances of marked seasonal periodicity for some species of parasitic worms. Such periodicity is usually attributable to seasonal changes in food habits of the host together with a limited life span on the part of the parasite. Since the present field investigation was carried on chiefly during the summer months, very little evidence of cyclical occurrence of parasites throughout the year has been obtained. However, it may be stated as a general principle that fish are most heavily parasitized at the season when they are most actively feeding. Those species which remain dormant and fast through the winter lose most of their parasites at this time. Other species, like the perch and pike perch which continue feeding during the winter, tend to retain their parasites through this season.

The parasites of fishes range from minute single-celled forms to the lamprey eels. While the protozoans are so very small that most of them can be seen only by the aid of a microscope, the lampreys are commonly about a foot in length. These two extremes in size represent the simplest and the highest groups of the animal kingdom (Protozoa and Chordata). By far the most abundant of the parasites affecting the fishes of the streams and lakes of temperate North America are midway between these two extremes, and represent the various groups of worms which have become adapted to a parasitic existence. There are five chief groups of these worms, differing widely among themselves in size, form, and structure and showing very pronounced individual preferences for different parts of the body of the host which gives them food and lodging.

These five groups of parasitic worms found in our fresh-water fishes are: (1) the flukes (Trematoda), (2) the tapeworms (Cestoda), (3) the thorny-headed worms (Acanthocephala), (4) the round worms (Nematoda), and (5) the leeches (Hirudinea). It is with the first four of these groups that the present study of worm parasites of the Oneida Lake fishes is concerned. The data on the leeches are incomplete, but may be considered in a later paper.

Under conditions of nature there is rarely a single individual fish, among all the numerous kinds, from the smallest minnows to the choicest game fishes, which does not harbor at least one or more species of worms somewhere in its body. Most often the fish parasites are confined to the viscera and hence are usually not noticed when the fish is dressed. But some of the parasitic worms take up their abode in other parts of the body of the fish. In the skin and even in the flesh they at times form conspicuous cysts or nodules, which render the fish unsightly, if not wholly unfit for human use. No organ or tissue is immune to attack.

Progress in the present survey was impeded by the relatively large number of unknown parasitic forms encountered. Of over ninety species of parasites collected in the course of this study, twenty-four have been described as representing new species, in Parts I and II. We also have several species of immature, or free living, nematodes mentioned in this report to which no names have been applied. One clearly new species of Ancyrocephalus has been left undescribed because of the unsatisfactory condition of the specimens available. One of our new species of Crepidostomum (*C. solidum*) was invalidated by the prior appearance of a description of the same species by Hopkins (1931) under the name *C. cooperi*. On the basis of a more extensive series of individuals, the writers are inclined to believe that *Neascus oneidensis*, named as a new species in Part I of this survey, is probably a synonym of the highly variable *Neascus vancleavei*, and it lately appears that *Allocreadium halli*, described as a new species in Part II, may be a synonym of *A. ictaluri* Pearse. To the best of the authors' knowledge the remaining twenty-one species described by us as new deserve recognition as distinct species.

The list of recognized species has grown until it far out-ranks that recorded in any previous survey of the fish parasites of any body of water within the United States. This is true with respect to both the list for individual host species and for the total faunal list of worm parasites encountered in the fish population of the lake as a whole. For example, Pearse (1924: page 193, table 3) has recorded eleven species of parasitic worms from *Perca flavescens* in a series of sixteen Wisconsin lakes, while in contrast we have a list of twenty-six species of worm parasites from this host in Oneida Lake alone. Similarly, in five Wisconsin Lakes, Pearse's survey of the parasites of all the fishes during two summers lists seventy-one species of worm parasites, whereas a list of more than ninety species has been prepared in connection with the survey of Oneida Lake. The exact number of species included in our work is difficult to determine at present because of the impossibility of evaluating the status of some of the larval forms, such as species of Tetracotyle and Diplostomulum. To the very end of our collecting additional species of parasites were encountered, even in those hosts which had previously been examined in large numbers.

In the main body of the report one section is devoted to a treatment of the individual species of parasites encountered in the field study. *In citing hosts, only those species actually encountered in the present survey have been included.* For most species of parasites a preliminary discussion of their taxonomic relations is followed by a brief description of the species. An analysis of the host and habitat relationships is given in as much detail as available information permits.

The final section consists of a list of parasites for each of the species of fish studied, and an analysis of our data from various other ecological angles. Especial attention is directed to the effect of food habits and environment in the determination of the parasitic population of each host species.

The Habitat.—*General character of the lake.*—A general description of Oneida Lake has been given by Adams and Hankinson (1928), to which the reader is referred for further details. The lake forms part of the New York State Barge Canal system, and lies in a general east-west direction, with the west end slightly more to the north than the east end. The chief streams entering the lake are Fish Creek and Oneida Creek, at the east end, and Chittenango Creek on the south shore near Bridgeport. Since such slow current as exists in the lake is from east to west, the eastern end is called the upper while the western is called the lower end of the lake. The single outlet of the lake is the Oneida River, at Brewerton, at the west end of the lake. Five miles below Brewerton the Caughdenoy dam raises the level of the river by about ten feet, backing up the water in the river and in Caughdenoy Creek, a tributary, and influencing to some extent the level of the west end of the lake. This dam is for the purpose of feeding the canal which branches off from the river about one and a half miles below Brewerton.

Large areas of swamp border the shores of the lake in its western portion. These extend from the north shore of Big Bay to Shaw's Point, inclusive; from north of Phillips Point to the eastern end of Three Mile Bay, inclusive, along the north shore of the lake; and on the south shore from Muskrat Bay around the shores of Lower South Bay to the edge of the village of Lower South Bay, inclusive. A smaller area of swamp borders the shore of Maple Bay. The map which accompanies this number should be consulted for general features and localities.

The two ends of the lake are very different in character. The lower section of the lake, west of Wantry and Long islands, has an irregular, indented shoreline with numerous sheltered weedy bays, projecting points and spits, and predominantly shallow water. The depth in this area varies from about 15 to 20 feet in the open water, and the bottom is chiefly of hard materials, sand, gravel, and boulders. In the middle and eastern sections the lake is wider and the shores are regular and steeper. Depth here varies in the open water from about 30 to 50 feet. The deepest part of the lake lies off the village of Cleveland where the greatest sounding is 55 feet. In this area the bottom is chiefly mud and clay. Occasional areas of gravel bottom occur, and at the eastern end of the lake large deposits of sand stretch away in a gradual slope from the shore. Boulder bars rise near to the surface at Dakin Shoals, Shackelton Shoals and Messenger Shoals. The greatest diversity of habitats is found in the western, shallow part of the lake. A great variety of conditions favorable to fish are found in the small bays along the indented shoreline. All types of aquatic vegetation abound in these protected waters, from dense stands of cat-tail rushes to thick growths of lily pads. Swamp loosestrife is a characteristic growth along the marshy shores, beyond which zone occur areas of arrow arum and other emergent vegetation. The shelter provided by these conditions is very favorable to certain types of fish. The bottom in the smaller bays varies in different localities from sand to mud. These features affect not only the fish life but also greatly influence the type of invertebrate life found in a locality, and all of these factors play a very large part in determining the establishment of parasites within a particular habitat. In the eastern and middle sections of the lake the regular outline and abrupt descent of the shores into the deeper water eliminate to a large extent such shoreline habitats and communities as are found in the western section of the lake. The fish which inhabit the first two sections are therefore chiefly such as seek the open, deeper waters. In the lives of these species the shelter of vegetation and protected shore waters play no part.

Methods.—*Collection of hosts.*—During the first two summers (1928, 1929) our base was at the Brewerton end of Oneida Lake, but headquarters were shifted to Cleveland for the summers of 1930 and 1931.

A motor boat and one or two rowboats formed part of our field equipment. All accessible parts of the lake were visited and fished instead of confining operations to a single region. This course was justified by the marked variety and diversity of habitat conditions previously mentioned, with their marked influences upon the fish and parasitic fauna present in any one locality. Our list of parasitic species continued to grow in proportion to the amount of new territory from which collections were made. If collecting operations had been any less extensive the results would certainly not have given any significant picture of fish parasitism in Oneida Lake.

In the field operations during the summers of 1930 and 1931, the fishes were examined immediately after being caught, or were kept living in live-cars until ready for examination, whereas during the summer of 1929, with few exceptions the fish remained several hours out of water after capture and were kept on ice over night before examinations were made. However, under both these sets of conditions, most of the parasitic worms were found alive and active when removed from the body of the host.

In the western area the seine and trammel net were used to advantage. The seine was chiefly useful along fairly clean sloping shores, whereas the trammel net was operated in weed-choked waters where no other method could have been applied. Gill nets had to be employed in the deeper waters of the middle and eastern parts, and traps were set along the shore. A beam trawl of the character designed and used with success by Dr. David H. Thompson, of the Illinois Natural History Survey, was operated in the deep water, and proved effective in securing certain species of fish, and especially smaller fish and the young of certain species inhabiting the lake bottom, which could not be obtained in any other way. Our specimens of ling, the bridled catfish (*Schilbeodes miurus*), tessellated darter (*Boleosoma nigrum olmstedi*), log perch (*Percina caprodes zebra*), the trout perch (*Percopsis omisco-maycus*), and the young of the silver bass (*Lepibema chrysops*) and of yellow perch were taken chiefly by the trawl. The results with the beam trawl, used by us for the first time in Oneida Lake, were sufficiently interesting and suggestive to justify the expectation that an intensive study of the deep water inhabitants by this method of collecting would yield much new and valuable information.

During the early part of June, 1931, some spearing was carried on along the shore of the lake west of Cleveland. During the winters, ice fishing was engaged in to some extent, in order to obtain winter records for some species. A few eels were collected by spearing, but most of our records for this species are on the basis of examinations of viscera obtained from the eel fishermen at Caughdenoy, where weirs have been constructed.

The larger adjoining streams of the lake were entered in our collecting operations and fished in their lower reaches. The Oneida River was seined as far as the Caughdenoy dam, and also Caughdenoy Creek, opening into the river a short distance above the dam. Big Bay and Three Mile creeks, tributary to Big Bay, were fished as far as navigable. Chittenango Creek was entered and collections made in a small tributary at the game protector's camp near Bridgeport. Black Creek, entering the lake at Cleveland, was fished at various points. A dam about 300 feet from the lake, confining a mill pond, prevents fish from passing upstream from the lake beyond this point, although fish must pass down over the dam at times of high water. A gill net stretched back and forth between the banks at the mouth of the stream caught numbers of suckers and ling. These fish had invariably been freshly attacked by lampreys, and for some unknown reason had sought to enter the cold waters of the stream as they were dying. The fish caught in this manner always came from the lake, being entangled on the outside of the net. There was no evidence of any migration downstream during the months of our operations. Frequently brown trout were also taken in this manner, and these were not always lamprey scarred, showing that normal impulses lead this species to move more or less at random from lake to stream and reversely.

The Cleveland mill pond, formed by a dam across Black Creek, has a soft mucky bottom. Water over a large part of its area is less than a foot deep. Gill nets set here secured numbers of a peculiarly dwarfed and emaciated common sucker (*C. commersonnii*), and also the brown trout (*Salmo fario*). Above the mill pond Black Creek is a typical trout stream, with a fairly steep course, passing through wooded land, with numerous shaded pools and rapids, and cold water. Collections of young brown trout were made at several points about one mile above Cleveland. Black Creek was the only trout stream we fished in this survey. There is evidence of a small population of brown trout existing in the lake, along the shores in the vicinity of the mouth of Black Creek, and in the Cleveland harbor, as frequently brown trout were taken in gill nets set off the harbor and behind the breakwaters at the village, although never found elsewhere in the lake.

We collected in the winding sloughs and backwaters of Fish Creek during the summer of 1931. We did not ascend the stream very far but confined our collecting to the sluggish waters near the mouth. Oneida Creek was not entered.

Examination of Hosts.—A physiological saline solution has commonly been employed in handling and examining living worms in work of this sort, but we found a solution of sodium bicarbonate, 7 grams to one litre of water (0.7 per cent) much more suitable. Its mildly alkaline reaction simulates conditions in the intestines and tissues of the host, and worms live and retain their normal appearance for a much longer period in this solution than in the ordinary saline solution. It further has the advantage of dissolving mucus and cleaning the worms more effectively than do solutions of common salt.

In some cases fishes were examined singly, in others collectively. A single host record number was given to collective examinations, but the number of fish included in the examination appears in parentheses after the host record number in all our records. The parasites were removed to separate dishes of soda solution, where, by their own active movements they quickly freed themselves from mucus. Smaller worms were handled with capillary pipettes, the larger with needles, forceps, or wooden applicators.

A great deal of labor and time are ordinarily expended in concentrating material, and to facilitate this process sedimentation and centrifuge methods were adapted to our requirements with great success. In order to free parasites of mucus the contents of organs were vigorously shaken in an 8- or 16-oz. bottle, with a liberal amount of soda solution, for two or three minutes, and the mass strained through a wire sieve to remove the coarser material and larger parasites, while allowing smaller worms to pass through. The sieve was then examined and any parasites caught were removed. The filtrate was set aside in a bottle for sedimentation. Parasites being heavier than organic débris rapidly sink to the bottom, whereas particles of mucus remain suspended for a long time. After decanting the upper layers of fluid the remainder was centrifuged, in several installments, if necessary. The sediment thrown down in the tubes was then removed to a Syracuse watch glass and examined in a little fresh soda solution under a Greenough type binocular microscope. This residue contains all the small worms, sometimes in great concentration, with a minimum of organic débris. By employing this method an examination can be made quantitative to within a very small percentage of loss, and actually at a great saving of labor and time over ordinary hand picking methods. In examining intestines, hearts, eyes, urinary bladders, etc., in this manner, the organs were opened and scraped and placed in the shaking bottle along with their contents.

Smaller fish and fry were frequently examined by teasing the entire body, and applying concentration methods. While this method had the disadvantage that we could not always be certain where the parasites came from, it saved a great amount of time. The work involved in examining separately the organs of a large number of small fish would have been prohibitive. The amount of labor involved in examining fish for parasites will be appreciated from the fact that an experienced worker can hardly handle more than four fish a day if these are examined singly. With collective methods a larger number can be gone over.

Killing and preserving.—Worms were thoroughly washed and freed of mucus before killing and preserving. Nematodes were fixed by dropping them into hot 70 per cent alcohol, which causes them to straighten. If the killing is carried on in a small vial the cork may be added and the material set aside, for the alcohol serves as preserving fluid also. The more delicate nematodes, such as Capillaria, and Philometra, are best fixed in cold Bouin's fluid. Heat causes these forms to shrivel.

Cestodes and trematodes give considerable trouble by contracting and thickening upon fixation, unless precautions are taken. We found that excellent results could be secured by applying to these worms a modification of the nematode technique, using hot Bouin's fluid in place of hot alcohol. The worms expand and die instantly upon striking the hot fixing fluid. This method not only saves a great amount of time but is an improvement over pressure flattening methods in that all specimens become uniformly expanded, and hence are properly comparable. What further flattening may be needed is done later on in the mounting process. Specimens were left in the Bouin's fluid for from 4 to 24 hours. They were then washed with several changes of 50 per cent alcohol until most of the yellow color had been removed, and transferred to 85 per cent alcohol for preservation. This entire process could usually be carried on in the preserving vial, and the liquids decanted or drawn off with a large pipette.

Acanthocephala must first be placed in tap water until they extrude their beaks, and may then be fixed by either of the above methods. Leeches are best fixed by the hot Bouin's technique. Parasitic copepods are best killed with cold 70 per cent alcohol.

Staining and mounting.—Most of our material was stained and mounted *in toto*. Sections were made only in connection with special problems since usually the general anatomy could be discerned from *toto* mounts. In nearly all cases our entire collections were mounted, instead of a mere sampling from each vial. We were thus able to study and review thoroughly every worm in our collection. The smaller worms frequently cannot be determined with certainty in alcohol, and wet specimens are awkward to handle.

Nematodes were mounted unstained in glycerine jelly, and the mounts sealed with euparal. Trematodes, cestodes and acanthocephalans were stained in Ehrlich's hematoxylin, borax carmine, or alum cochineal. After destaining, neutralizing, and washing in 70 per cent alcohol, specimens requiring further flattening were placed between glass slides tied together under the proper amount of pressure, and these slides placed in a jar of 100 per cent alcohol. After 24 hours the slides were removed to a petri dish of 100 per cent alcohol, the specimens released and transferred to cedar oil for further clearing, and then mounted.

Acanthocephala may be mounted in the same way as flatworms, but before staining should be punctured in several places to avoid developing a "vacuum opacity".

Whole mounts do not develop their maximum transparency until several months after preparation, because of the time required for the balsam to diffuse evenly through the object and to harden to an increased refractive index with greater clearing power.

Summary of Hosts Examined.—The following list presents a summary of the field operations in terms of number of species and number of individuals of fishes examined for parasites. The scientific and common names employed are the same as those appearing in Adams and Hankinson's "Ecology and Economics of Oneida Lake Fish" (Roosevelt Wild Life Annals, Vol. I, Nos. 3, 4).

Name of Fish	Number Examined
1. *Petromyzon marinus:* Lake lamprey	12
2. *Amia calva:* *Bowfin	1
3. *Leucichthys artedi tullibee:* Tullibee	24
4. *Salmo fario:* Brown trout	16
5. *Catostomus commersonnii:* Common sucker	36
6. *Erimyzon sucetta oblongus:* Chub sucker	6
7. *Cyprinus carpio:* Carp	9
8. *Leucosomus corporalis:* Fallfish	6
9. *Notemigonus crysoleucas:* Golden shiner	29
10. *Hybognathus regius:* Silvery minnow	40
11. *Pimephales promelas**:* Blackhead minnow	3
12. *Ictalurus punctatus:* Spotted catfish	3
13. *Ameiurus nebulosus:* Common bullhead	82
14. *Ameiurus natalis:* Yellow bullhead	4
15. *Noturus flavus:* Stone cat	1
16. *Schilbeodes gyrinus:* Tadpole cat	17
17. *Schilbeodes miurus:* Variegated stone cat	4
18. *Umbra limi:* Mud minnow	14
19. *Esox niger:* Chain pickerel	68
20. *Esox lucius:* Common pike	19
21. *Anguilla rostrata:* Eel	87
22. *Fundulus diaphanus menona:* Barred killifish	2
23. *Percopsis omisco-maycus:* Trout perch	187
24. *Lepibema chrysops:* White bass	21
25. *Perca flavescens:* Yellow perch	273
26. *Stizostedion vitreum:* Pike perch	56
27. *Percina caprodes zebra:* Manitou darter	22
28. *Boleosoma nigrum olmstedi:* Tessellated darter	25
29. *Micropterus dolomieu:* Small mouth black bass	20
30. *Micropterus salmoides:* Large mouth black bass	44
31. *Eupomotis gibbosus:* Common sunfish	61
32. *Ambloplites rupestris:* Rock bass	20
33. *Pomoxis sparoides:* Calico bass	7
34. *Lota maculosa:* Ling or burbot	8
Total number of examinations	1,227

* Taken from Cross Lake, New York.
** Taken from Colvin Street Ponds, Syracuse, New York.

The lack of balance between the numbers of different species examined is chiefly a reflection of their relative abundance in the lake. The yellow perch is probably the most abundant food fish in the lake and in consequence we have examined more perch than any other species. In the work of examination we were largely governed by what we could get. Percopsis is evidently extremely abundant in the deep waters of the lake. We caught it in great numbers in the beam trawl, and a large number of individuals were examined. On the other hand our examinations of some species were regrettably low. A case in point is the catfish, *Ictalurus punctatus,* in which instance we were limited to three specimens obtained from carp fishermen. We secured no specimens of this fish in our own collecting.

Adams and Hankinson, in their Ecology and Economics of Oneida Lake Fish, (1928), list 58 species known to occur in Oneida Lake, and also add a hypothetical list of 19 species, which for various reasons they supposed to inhabit the lake, although they had secured no specimens. Comparing our host list with Adams and Hankinson's list of fishes, the fact appears that we have one species, *Noturus flavus,* which they do not include. Our record is based on a single specimen taken while spearing west of Cleveland, June 12, 1931. One of our species is included in the above authors' hypothetical list—*Salmo fario. Pimephales promelas* probably does not occur in the lake but is mentioned in the text in connection with our discussion of Clinostomum. *Amia calva,* as mentioned above, occurs in the lake, although our single specimen was obtained from Cross Lake. Excluding *Pimephales promelas* our list includes thirty-two species of fish from the lake and its immediately adjoining waters, embracing practically all of the more important fish in the lake. Species not represented are chiefly forms mentioned in Adams and Hankinson's hypothetical list, which are either of very rare occurrence in the lake or totally absent from it; and also several of the smaller forms, chiefly minnows, listed by the above authors as actually occurring in the lake. The parasitic fauna of these smaller fishes consists chiefly of larval stages embedded in the musculature, awaiting transfer to some further host, or immature stages in the intestine acquired from the plankton. There is not the same degree of diversity and specificity in the parasitic fauna of many of these small fishes which obtains in the case of the larger fish, and in all probability we missed very little by not including these remaining small forms. All of the important food fishes have been covered in this survey.

The Literature on Fish Parasites.—Though fish parasites have been very extensively investigated in North America, especially since the opening of the present century, there have been but few intensive studies partaking of the nature of faunal or ecological surveys. The field of systematics has been so fertile that most investigators have become engrossed in the descriptions of new species and genera which almost invariably make their appearance, even in small collections. Until recently, the scattered and inaccessible condition of the literature on parasitic worms rendered the identification of general survey collections extremely difficult.

A handbook on fish diseases by Bruno Hofer (1906) offered to students of fish and fish-culture a condensed treatment of the more common fish parasites of Europe and gave impetus to the study of fish diseases. A more recent similar work by Miss Plehn (1924) has had wide use as a reference book. Aside from non-technical descriptions of some of the more common genera of fish parasites, neither of these works has more than a limited application for students of the parasites of American fishes. No similar handbook has ever been prepared to cover the parasitological problems of interest to fish culturists in North America. Small treatises of very limited scope have, however, appeared in the literature, as samples of which "The care and diseases of trout" by Davis (1929) and "The treatment of fish diseases" by Moore (1929) may be cited.

Following the rapid growth of the special literature on parasitic worms, especially by European writers, a distinct service was rendered to American biologists by Dr. H. S. Pratt (1902) through his keys and drawings of trematodes in the American Naturalist series of Synopses of North American Invertebrates. At that time there was no adequate conception of the degree of distinctness or relationship between the North American and European faunas. In Europe, Brauer's "Süsswasserfauna Deutschlands" with the admirable sections by Max Lühe on Trematoda (1909), Cestoda (1910), and Acanthocephala (1911) provided a convenient organization of the information in the rapidly expanding field of systematics. In these volumes were assembled for the first time a critical evaluation of the genera and distinctive characterizations of species of the European fauna. This work laid the foundation for exact comparisons between the species of parasitic worms from the European and American continents, for critical synoptic treatment of the American fauna was hardly possible until after the older European species had been re-studied and evaluated in detail. In 1918, Dr. Henry B. Ward made a contribution to the literature in the chapters of Ward and Whipple's "Fresh-Water Biology," which inaugurated a new era for the general student of parasitology in that a critical analysis of the literature and a synthetic survey of all the parasitic worms known to occur in fresh-water hosts of this continent were presented for the first time.

Prior to this era, the pioneer workers had been amassing descriptions of new genera and new species and numerous erroneous assumptions of synonymy based upon imperfect understanding of the older European species and misconceived notions of host specificity. The service rendered in the interpretation of this literature has materially lightened the burdens of students of the present generation.

A survey of the early literature reveals no parallels for the fresh-water fauna comparable to the works of Linton on the parasites of marine fishes of the Atlantic Coast (1889-1914). Leidy's contributions (1851-1890), valued though they are, were chiefly records and descriptions of individual new forms with little concern for the completed picture of the parasite fauna of a given region. During the early period of growing interest in helminthological investigations, there were some contributions of value which considered the parasites of a limited number of host species, and some which were rather clearly regional studies on distribution. Unfortunately, the results of most of the last mentioned surveys were presented as simple statistical tabulations of percentages of infestation by the various classes of parasites with rarely a determination to the genus and practically no specific identifications of the parasites found. The outstanding publications distinctive of this period were those of Linton (1889-1914), Ward (1894-1918), Stafford (1900-1905), Marshall and Gilbert (1905), and Osborn (1902-1919). The papers of these authors added materially to the lists of known genera and species for the continent and furnished the first ground for an understanding of the faunal and distributional relations of parasites and their hosts. Cooper (1915), following the precedent of some earlier Canadian zoologists, made meritorious contributions to the field study and biology of fish parasites from Canadian waters. Ward's extensive regional studies (1894-1918) resulted in the tabulation of percentages of infestation of large numbers of the Great Lakes fishes by the various classes of worm parasites. Many facts of host preferences and limitations were revealed by these statistical methods, but specific identifications of the collections forming the basis of the studies were never published. More recently, Essex and Hunter (1926) have published similar statistical results modeled on the early papers by Ward.

Intensive taxonomic studies in this country have been, for the most part, devoted to monographs on the morphology and taxonomy of restricted groups. These monographic revisions rarely transgress the bounds of a single family or class. Most of them have been inspired and made possible by the admirable organization of the available materials in the helminthological chapters of the *Fresh-water Biology,* and in large measure the researches on parasites of aquatic animals of this continent have been conducted by the students of Henry B. Ward. Many of the monographic studies on limited groups give valued information on the biology and host relationship of the forms considered, but faunistic and ecological treatises dealing with the parasitic fauna as a whole are extremely few. Pearse (1924, 1924a) has studied the parasites of fishes in the upper Mississippi River and in Wisconsin Lakes, with a detail of biological and ecological analysis never before attempted in this country.

The ecological aspects of fish parasites and their relations to the host have recently received the attention of Holl (1932) who for a limited number of species of fishes and amphibians has attempted an ecological analysis of the parasite fauna.

Bangham (1925, 1927b) has carried on extensive studies, especially on the tapeworms of the black bass and on the problems of parasites in their relation to fish hatcheries in Ohio (1927).

Hunter (1928, 1929, 1930, 1932, 1932a) has published extensively on the parasites of fishes, directing his attention primarily to the tapeworms and their developmental cycles. Especially in connection with the program of studies for the New York State Conservation Department, Hunter and Hunter (1929, 1930, 1931) have collaborated in studies on parasite surveys for a number of areas within the State of New York.

In the analysis of his own results, Pearse (1924a) has called attention to the obstacles confronting the student of the ecology of fish parasites, and has expressed the belief that, "Before all the factors which influence parasitism in fishes are known, if they ever are, parasitologists and ecologists will have to labor for several generations". With this view the present authors are inclined to coincide.

Biology of Fish Parasites.—*Mode of Infestation.*—When they first begin to take food, the fry of many fishes start to accumulate a parasitic population within their bodies. The food habits of a fish, and many of the conditions of its environment, influence the number and nature of the parasites which it will carry. So definitely are the habits of the fish correlated with its parasitic fauna that Ward in one of his pioneer studies (1910:1161) stated as a generalization: "The parasitic record reflects clearly the manner of life led by any host", and further (p. 1191): "The parasitic fauna of any animal is primarily a function of its habitat".

Regardless of the feeding habits of the adult, most of the fresh-water fishes for a while after birth feed upon plankton. Since plankton organisms serve so commonly as hosts for larval worms the young fish feeding on plankton are peculiarly open to invasion by these larval parasites. The young of fishes not infrequently have parasitic populations unlike those of the older ones of the same species and these dissimilarities may be traced directly to differences in food habits at different ages.

Weedy bays with mud bottoms yield a high incidence of trematode infestations in fishes because these conditions offer favorable habitat to a snail fauna, and snails are the chief hosts of larval trematodes.

In an analysis of the host-parasite-habitat relationship of the trematode type involving one species of vertebrate host, one species of trematode, and one species of snail, there are three areas of distribution to be considered: the range of the vertebrate host, the range of the snail host, and the range of the parasite. Usually the ranges of the larval and definitive hosts do not coincide exactly. Under these conditions the range of the parasite is limited to areas where its hosts overlap. Migratory movements and random wandering of fishes prevent the establishment of absolute limits to such areas of parasite distribution, but they are fairly clear in a number of instances in Oneida Lake.

Roughly speaking, there are only two chief avenues by which worm parasites gain their position within the host, (1) passively, as when taken in along with food, and (2) through active migration on the part of the parasite. Active migration involving the penetration of tissues occurs most often among the trematodes and cestodes. But regardless of the method of entry into the final host, many parasitic worms have the power of migration through tissues at some stage in their development.

Woodhead (1930) has witnessed the active penetration of the skin of fish by larvae of Bucephalus, and it is known that similar penetration through the skin is fairly common among trematode parasites of other vertebrate hosts. Some immature worms liberated in the digestive canal actively burrow through muscles, liver, and other tissues until they come to lie in favorable location within the body of the host.

More or less passive migration takes place in a few fish parasites as for example in the blood fluke (Sanguinicola) which may be carried from the heart to the gills or other organs by the blood stream. The eggs of a European species of Sanguinicola have been found to possess sharp cutting spines. These eggs, also carried passively by the blood stream, break through the walls of capillaries by means of the spine, especially in the gills and the urinary bladder, and thus leave the body of the fish. This adaptation increases the chances of the egg to reach the outside world and to come into contact with a snail suited for its development.

Effect upon the host.—Little is known concerning the effects of worm parasites upon fish. There are a few references in the literature regarding the association of worms of various genera with epidemics among fish. Pratt (1919:1), in remarking in general on fish parasites, has stated that they occasionally are the cause of disastrous epidemics in which thousands of fishes die. Opposed to statements such as this are the opinions of others who think that most fish parasites do but little damage. For example, Pearse (1924:187) states, "Most fish parasites do little harm to their host".

Epidemics most often occur in fish hatcheries and rearing ponds where conditions for excessive propagation of parasites are provided by two outstanding factors—overcrowding and live food. The factor of overcrowding is conducive especially to the appearance of ectoparasitic trematodes, many of which demand only intimate association of susceptible hosts to ensure infestations approaching epidemic proportions. Thus members of the genus Gyrodactylus become a menace in hatcheries (Van Cleave, 1921; Guberlet, Hansen, and Kavanagh, 1927; and others) while members of the same genus offer serious handicaps to goldfish culture, where their presence is diagnosed as "fin disease".

When living food is furnished to fry and fingerlings, the stock of forage fish and reared crustaceans always offers opportunity for serious outbreaks of parasitic infestations. At Neosho, Mo., the United States Bureau of Fisheries encountered serious obstacles to bass culture through the introduction of larval tapeworms with the food. Similar instances are not uncommon in state and private hatcheries, and in the literature (Hunter, 1928) there are records of degenerative changes in the ovaries producing sterility as a consequence of infestations by tapeworm larvae, which entered the host by way of infested live food.

Fish Parasites and Human Disease.—Recently there has been wide publicity over the possible relation of fish to human disease. In a considerable number of regions of North America, one of the human tapeworms, known as the fish tapeworm of man or the broad tapeworm (*Diphyllobothrium latum*), passes a part of its life in the flesh of food fishes. No larvae of the broad tapeworm have been found in the fishes of Oneida Lake, but there are records of occurrence within the state of New York.

Mueller (1933) has recorded a new species of Diphyllobothrium from the Oneida Lake area where it appears to be common in cats. This form is markedly different from *D. latum* in size and anatomical characters. The life history has not as yet been worked out, and consequently it is not known whether the larvae occur in fish, or can produce infestation in man.

In North America, the broad tapeworm is the only parasite known to be transferred to man through eating fish. None of the parasites of fishes described in this paper can be transmitted to man.

Control Measures.—In hatcheries and rearing ponds, where breeding stock and young are kept under controlled conditions, programs of extermination of dangerous parasites may be inaugurated with success. Ponds and tanks may be treated chemically to destroy pests, and even fishes may be subjected to dips like those administered to domestic animals for the removal of external parasites. The food supply may be controlled to eliminate sources of infestation by internal parasites. These and many other measures are available to prevent dissemination of injurious parasites through distribution of fish from hatcheries and rearing ponds. However, under conditions of nature, especially in streams and large lakes, control measures for the elimination or even the reduction of infestation have never been practicable.

A few control measures for natural waters have at times been advocated. For one private lake where trout were seriously damaged by cysts of the larval trematode Clinostomum, Linton (1911) advocated the shooting of water birds which carried the adult flukes. At one time the extermination of pelicans from Yellowstone Lake was advocated to relieve the introduced trout from serious epidemics of larval tapeworms which reach maturity in the pelican. Obviously such control measures as depend upon the extermination of any group of animals is indefensible from the point of view of conservation, and wholly impossible of application except in very restricted areas.

The adjustment between a parasite and its host is so delicately balanced that epidemics of injurious parasites under conditions of nature rarely have a lasting influence upon the host species. Wholesale destruction of the host spells ultimate destruction of its dependent parasites. Consequently an epidemic is followed by a period of relative freedom from the species which caused the high mortality in its host. Thus the balance of nature is maintained and the well adapted parasite never causes the extermination of its host species nor does nature permit the host to become wholly free from its parasites.

As a control measure for the elimination of flukes from domestic animals, Chandler (1920) proposed the extermination of snails from the waters of the infested territory, since snails are essential for the development of the larvae of flukes. Baker (1922) pointed out the serious consequences of such a program even if it were capable of execution. Snails play such an important role in the food chains of aquatic organisms that the removal of this one form of life would upset the entire economy of the stream or lake in question.

Practical control measures have been developed for only a few of the many species of fish parasites. Though almost without exception the procedures recommended apply to cultural practice solely, these have been cited in the body of the present report under the respective genera and species of parasitic worms.

SECTION 2.—TAXONOMY AND BIOLOGY OF THE TREMATODA OF ONEIDA LAKE FISHES

The trematodes are more abundantly represented than any of the other groups of parasitic worms in our collections, both in number of species and number of individuals. The forms which we have collected from fishes fall into two distinct biological groups: (1) those which attain sexual maturity in or on the body of the fish; and (2) those which are immature in the fish and reach functional sexual activity only when introduced into some fish-eating animal. This final host of the larval trematodes found in a fish is usually a bird or a mammal, though in some instances larvae in the body of one fish may represent developmental stages in the life cycle of species which reach maturity in fishes that feed upon their own kind.

The trematodes or flukes are almost always hermaphroditic worms with the body usually somewhat flattened dorso-ventrally and carrying a single set of reproductive organs. In all trematodes there are digestive organs consisting of a mouth connecting with a tubular portion which usually divides into two lateral branches though the relative development and specialization of the parts differ profoundly in different members of the class. One or two suckers for attachment are commonly present, though lacking in some flukes living on the skin or gills (Monogenea), where grappling hooks and spines are developed for fixation. In most trematodes, one of the suckers surrounds the mouth and is known as the oral sucker, while the other is known as the ventral sucker or acetabulum.

The adult trematodes of fresh-water fishes occur most commonly in the digestive tract, but one genus (Acetodextra) lives in the air bladder and another (Phyllodistomum) in the urinary bladder. Up to the present time, a single genus has been found in the heart and blood vessels of our fresh-water fishes. This is the genus Sanguinicola, reported from this continent for the first time in Part I of this series. All of the foregoing trematode parasites infesting the internal organs belong to the subclass of Trematoda known as the Digenea, and agree fairly closely in character of the life history. At least one other sort of animal besides the fish is needed for the development of the Digenea or digenetic trematodes. When a single alternative host is used by the trematode, this is invariably a mollusk and usually a snail. The egg produced by the adult worm hatches into a larva (the miracidium) which dies if it fails to find a suitable mollusk into whose body it can penetrate. Only certain species of snail are suited to serve as host for a definite species of trematode in just the same way that most of the adult fish trematodes can live normally in the bodies of only one or a few species of fish.

Within the body of the snail each larval trematode which enters undergoes growth and reproduction through a complicated series of stages which finally give rise to young trematodes capable of becoming established in the body of a fish. Thus there are two reproductive cycles, one in the body of the snail and the other in the fish, so there is said to be an alternation of generations accompanying an alternation of hosts.

While by far the greatest number of fresh-water fish trematodes belong to the Digenea, there are some others which live on the gills and fins of fishes and there undergo direct development. The young worms, as soon as born, may become attached to the body of the same kind of fish which sheltered the parents, and there spend their entire life. These are known as the Monogenea or monogenetic trematodes. While a number of genera of these monogenetic trematodes are known from American fishes, but four genera have so far been found in our Oneida Lake survey, infesting the gills of various hosts.

Artificial Key to the Genera of Adult Trematodes of Fresh-water Fishes of North America

(* Denotes genera found in Oneida Lake.)

1 (a) Living on the skin, fins or gills of fishes (Order Monogenea) 2
(b) Living in the internal organs of fishes (Order Digenea) 6
2 (a) Posterior tip of body modified as a single adhesive organ 3
(b) Posterior tip of body provided with more than one sucker 5
3 (a) Attachment organ with two large hooks 4
(b) Attachment organ with four large hooks .... Sub-family **Tetraonchinae***
(The genera of this subfamily are so numerous, and the native members so inadequately known at present, that it is not feasible to give a key to the genera here.)
4 (a) No eyes present, 16 marginal hooklets .... **Gyrodactylus***
(b) Two pairs of eyes present, 14 marginal hooklets .... **Dactylogyrus***

5 (a) Posterior tip of body provided with one median sucker having four hooks and lateral suckers each with a single hook.......................... **Diplobothrium**
(b) Posterior tip of body provided with eight suckers, in two marginal rows of four each, each sucker with a chitinous armature.............................. **Discocotyle**
(c) Posterior tip of body provided with a large number of small suckers arranged in two rows, each sucker with a chitinous armature...................... **Microcotyle**
6 (a) With a prominent complete circle of spines surrounding the mouth.............. 7
(b) Mouth not surrounded by a circle of prominent spines........................ 8
7 (a) Ventral sucker and genital pore in posterior half of body, far behind the fork of the intestine .... **Allacanthochasmus***
(b) Ventral sucker and genital pore in anterior region of body, near fork of intestine .... **Neochasmus***
8 (a) Digestive tract not associated with anterior sucker............. Family **Bucephalidae***
(A key to the genera of this family is given in the text, p. 185).
(b) Anterior sucker opening into the digestive tract.............................. 9
9 (a) Oral sucker surrounded by papillae.. 10
(b) No papillae surrounding the oral sucker.................................... 11
10 (a) Uterus tubular, not reaching to posterior extremity of the body..... **Crepidostomum***
(b) Uterus an expanded sac, usually reaching to posterior extremity.......... **Bunodera***
11 (a) Ventral surface of body modified as an adhesive organ, divided into a number of alveoli 12
(b) Ventral surface not modified as an adhesive organ............................ 14
12 (a) Alveoli of adhesive organ arranged in four longitudinal rows........... **Aspidogaster**
(b) Alveoli of adhesive organ arranged in three longitudinal rows.................. 13
13 (a) Adhesive organ oval or elliptical, mouth subterminal. Testis single........ **Cotylaspis**
(b) Adhesive organ oval or elliptical, mouth terminal. Testes two........... **Cotylogaster**
14 (a) With no ventral sucker. Testis a paired median series of follicles. In heart and blood vessels .... **Sanguinicola***
(In this form the mouth is at the anterior end of the body, but the oral sucker is rudimentary or absent.)
(b) With a ventral sucker. Testes two in number................................ 15
15 (a) Genital pore on or near left margin of body.................................. 16
(b) Genital pore on left margin of acetabulum................................... 20
(c) Genital pore anterior to acetabulum, on or near median line..................... 21
16 (a) Uterus not extending to posterior end of body................................ 17
(b) Uterus extending to posterior end of body................................... 18
17 (a) Vitellaria extend from region of acetabulum, or in front of it, to the posterior extremity. Cirrus sac lies wholly, or mostly, in front of the acetabulum.......... **Plagioporus**
(b) Vitellaria limited to a short median zone just back of the acetabulum. Cirrus sac extends behind acetabulum.. **Plagiocirrus***
18 (a) Testes oblique .... **Alloplagiorchis**
(b) Testes serial, in mid line... 19
19 (a) Ovary three lobed .... **Triganodistomum***
(b) Ovary many lobed.. **Lissorchis**
20 (a) Cirrus sac present, transverse, anterior to acetabulum. Minute, pear shaped worms, with spinose cuticula .... **Maritrema***
(b) Cirrus sac lacking. Seminal vesicle and prostate glands free in parenchyma anterior to acetabulum. Globular worms of moderate size with smooth cuticula.. **Microphallus***
21 (a) Body leaf-like, divided into a disc-like hindbody, and a narrow cylindrical forebody. In urinary bladder .... **Phyllodistomum***
(b) Body elongate, or ovoid, not divided... 22
22 (a) Cirrus sac present.. 23
(b) Cirrus sac absent 26
23 (a) Ovary many lobed, or follicular, near dorsal surface. Testes lateral. Minute, broad worms with notched posterior margin.............................. **Vietosoma***
(b) Ovary rounded, testes serial or oblique, form elongate.......................... 24

24 (a) Uterus limited to space between anterior testis and acetabulum, vitellaria from pharynx to posterior tip .... **Allocreadium***
(b) Uterus passes to posterior tip of body, vitellaria lateral in mid region............ 25
25 (a) Spination delicate, esophagus short or absent........................ **Alloglossidium***
(b) Spination coarse, esophagus long................................. **Macroderoides***
26 (a) Sinus on anterior lip of acetabulum, enclosing the genital pore and a solid muscular organ, the gonotyl.. 27
(b) No gonotyl present, genital pore opening on surface............................ 28
27 (a) Large flattened worms, vitellaria lateral, in posterior half, acetabulum slightly dextral, inhabitants of air bladder of silurids................................ **Acetodextra***
(b) Small cylindrical worms, vitellaria in median third.................. **Cryptogonimus***
28 (a) Vitellaria a small cluster of few large follicles at extreme posterior tip..... **Halipegus**
(b) Vitellaria a cluster of follicles in extreme anterior region, at level of pharynx .... **Caecincola***
(c) Vitellaria of greater longitudinal extent, and encroaching upon mid region of body. 29
29 (a) Ovary a rosette of numerous lobes in center of body............. **Centrovarium***
(b) Ovary whole or rounded... 30
30 (a) Uterus of considerable longitudinal extent, forming a long series of transverse loops in intercrural space from acetabulum well into posterior region of body.. 31
(b) Uterus restricted to a few coils immediately posterior to acetabulum........... 32
31 (a) Testes immediately posterior to acetabulum and anterior to uterus. Ovary in caudal region posterior to uterus.. **Leuceruthrus**
(b) Ovary and testes in close contact in caudal region posterior to uterus........ **Azygia***
32 (a) Ovary on posterior edge of acetabulum, testes lateral, in mid region of body .... **Microcreadium**
(b) Ovary on posterior edge of acetabulum, testes serial in posterior half of body .... **Anallocreadium**

Since the completion of Part III, the following additional genera have been found in Oneida Lake: Plagioporus, Creptotrema, Octomacrum, Cleidodiscus, and Urocleidus. See Part IV.—Mueller.

Most of the larval trematodes found in Oneida Lake fishes represent developmental stages in the life cycle of worms of which the adult stages are wholly unknown. Many of them belong to the family known as holostomes or Strigeidae which attain maturity in fish-eating birds and mammals, but the complete, specific life history is known for but a small number of these holostomes. It is probable that some of the known adults in birds and mammals and larvae from fishes may belong to the same species. Though much work has been done on the holostomes by La Rue and other workers in his laboratory, these investigations have succeeded in tying only a few of the larval and adult stages together with conclusive evidence of identity.

The larval flukes from fishes all belong to the group of digenetic trematodes which means that the worms have lived in the body of a snail before they reach the tissues or organs of the fish. The species most commonly observed are those which become encysted in the skin. Here they appear as boil-like swellings (Clinostomum) or as dark pigmented spots (Diplostomulum) on the skin, especially in the regions of the fins. Often the microscopic holostome cysts are so numerous that the skin of the fish feels rough to the touch. The large, yellowish or cream colored cysts of Clinostomum shelter the young of worms which reach maturity in some of the water birds. These cysts occur in deep-seated tissues as well as in the skin. When ruptured, a worm of considerable size emerges.

Minute trematode cysts are often scattered through the body, but usually each species has preferential locations. Members of one genus (Tetracotyle) occur especially in groups of cysts on the heart, while still another is especially abundant on the mesenteries and in the liver and kidneys (Neascus). Within the muscles many minute cysts are found, some of which are holostome larvae while others are clearly the immature young of Allacanthochasmus or of Centrovarium. It is not uncommon for both encysted and free larval trematodes to be encountered at the same time in the digestive tract, having come from the digested bodies of their natural hosts. Miss Butler (1919) has called attention to the occurrence of larval trematodes in the eyes of fish; and other investigators have since then worked on the problem. Several species of holostome larvae live in the lens and in the humor of the eye where they move about with considerable freedom, and apparently little inconvenience to the fish. In some instances these larvae are so very abundant that they may be seen squirming within the lens before the eye is cut.

As a means of recognizing the genera of these larval trematodes of fishes, individual species of which are discussed in detail in another section of this paper, an artificial key to the genera known to infest fresh-water fishes of America is appended to this section. In this key no consideration is given to larval forms from the lumen of the digestive tract, representing species which reach maturity in the same location. In any extended collecting, intergrading series of the young and adult worms will be found and their identity readily recognized.

ARTIFICIAL KEY TO THE GENERA OF IMMATURE TREMATODES OF FRESH-WATER FISHES OF NORTH AMERICA

(* Denotes genera found in Oneida Lake)

1 (a) Sexually immature trematodes within a cyst 2
(b) With no cyst surrounding the immature worm 7
2 (a) Ventral surface of body furnished with a hold-fast organ in addition to the acetabulum (Family Strigeidae) 3
(b) With no attachment organ other than acetabulum on the ventral surface 5
3 (a) Body conspicuously constricted to form two divisions, a forebody and hindbody 4
(b) Body lacking definite division into forebody and hindbody .... **Tetracotyle***
4 (a) Anterior margin of body provided with two lateral sucker-like organs. **Diplostomulum***
(b) With no lateral sucker-like organs on anterior end of body .... **Neascus***
5 (a) Mouth surrounded by a circle of oral spines .... **Allacanthochasmus***
(b) No conspicuous circle of spines about the mouth 6
6 (a) Rudiment of ovary anterior to testes .... **Centrovarium***
(b) Rudiment of ovary between testes .... **Clinostomum***
7 (a) Body conspicuously divided into fore- and hindbody, and in addition to acetabulum carries a ventral hold-fast organ. Usually in eyes of fishes .... **Diplostomulum***
(b) Body long and narrow, sides practically parallel with only slight constriction to form a waist. Acetabulum the only ventral hold-fast organ. In gut or flesh of fishes .... **Apophallus***

Trematoda: Order Monogenea

FAMILY GYRODACTYLIDAE

Four distinct species of monogenetic trematodes belonging to the family Gyrodactylidae have been encountered on the gills and skin of Oneida Lake fishes. Three of these four species have been described as new in Parts I and II of this survey, while the fourth comprises the record of a species common to the European and American continents. Four distinct genera are represented by the species found in Oneida Lake and these represent all of the genera of this family which have been reported from fresh-water fishes of North America.

A survey of the literature emphasizing the scarcity of records for members of the Gyrodactylidae has been given in Part II of this report (Mueller and Van Cleave, 1932:91). The small size of the worms and the ease with which specimens on the gills and skin may be overlooked are the chief factors responsible for the scanty information available. In some of the most comprehensive surveys of fish parasites that have been made in this country the gyrodactylids have been left entirely out of consideration. Thus Pearse (1924:161) in his studies on the parasites of lake fishes has given the most detailed information on the parasitic worms that is available for the fresh-water fishes of any locality in the United States, yet in his published lists he has not directly mentioned the occurrence of the gyrodactylids. Holl (1932) has recorded the occurrence of an unnamed species of Ancyrocephalus on the gills of three species of the sunfish family, in his study on the ecology of fish parasites. According to Holl (1932:95), this undetermined Ancyrocephalus was restricted to the months of March and April.

Because of their direct development, never involving intermediate hosts for the larval stages, infestations may become greatly increased in a relatively short time. For at least some species of the genus Gyrodactylus, the development becomes very much telescoped, thereby increasing the rate of multiplication inordinately. Paedogenetic young within the body of the hermaphroditic parent may in turn bear developing eggs or young until at least four generations are readily distinguishable, existing simultaneously, one encased within another. Under such a set of conditions the young at birth is almost immediately ready to produce another individual. Because of this special adaptation to rapid reproduction, outbreaks of epidemic proportion are especially likely to accompany the crowded conditions of fishes under cultural management in fish hatcheries and rearing ponds. From these sources gyrodactylid worms may be disseminated when infested fishes are planted in native waters previously uncontaminated by skin and gill parasites. Under conditions of nature, in open waters, we have never encountered infestations heavy enough to cause obvious injury to the hosts.

W. N. Hess (1930:131), who has made rather extended observations on Gyrodactylidae, states that "members of the genus Ancyrocephalus were also found on sunfish, perch, and small mouth and large mouth black bass, both in Indiana and in central New York. The economic importance of Gyrodactylus parasites has been well demonstrated, and members of the genus Dactylogyrus have been reported as being very destructive in certain parts of Europe. These latter parasites have already caused serious losses among goldfish in this country and experiments are under way which indicate that members of the genus Ancyrocephalus, and to a certain extent those of Dactylogyrus, are destructive to certain nest building fishes, not only in hatcheries but also in open ponds and streams." To the present, no detailed information on the destructive nature of these skin and gill parasites is available for other than cultural conditions.

A total of five species of fish have been found carrying natural infestations of gyrodactylids in Oneida Lake. Our records support the view that gyrodactylids in Oneida Lake are rigidly limited in their host relations.

Genus Gyrodactylus Von Nordmann, 1832

The members of this genus are very imperfectly known for North America. In a few instances where outbreaks have been recorded no attempt has been made to designate the species of Gyrodactylus involved. The genus seems to be very widely distributed on this continent for the literature contains accounts of specimens from Canada, Maine, Washington, New York, and a number from the North Central States.

It is known that under cultural conditions and overcrowding, members of the genus Gyrodactylus may assume important roles, causing death of the host (Van Cleave, 1921; Hess, 1928, 1930; Guberlet, Hansen and Kavanagh, 1927).

We have found a single species of Gyrodactylus (*G. cylindriformis*) in the Oneida Lake region. This was described in Part II of this survey, to which the reader is referred for a description of the species.

Hess (1930) has recorded experiments wherein he determined that potassium permanganate is the most effective of the chemicals which have been tried for treating fish to remove Gyrodactylus. He found that one pound of potassium permanganate to 32,000 gallons of water may be used effectively in clean tanks of either cement or steel. This dosage resulted in removal of the flukes within two hours. In wooden tanks and in ponds the organic materials reduce the permanganate and render treatment less effective. Hess's directions for treatment of infested ponds call for spraying the surface of the pond with a solution of potassium permanganate in the above-mentioned strength. Parasitized fishes habitually seek the surface, hence come into contact with the concentrated solution before it becomes diffused through the deeper water where the organic matter breaks it down.

Gyrodactylus cylindriformis Mueller and Van Cleave, 1932

Host.—*Umbra limi,* on skin.

This species has been recorded but once, on the basis of specimens found in the Oneida Lake survey. So far as our observations go, it is limited in its host relations to the mud minnow (*Umbra limi*). Though Adams and Hankinson (1928:386) record the capture of the mud minnow from the waters of Oneida Lake, we have never taken specimens from the lake proper. From a collective examination of five specimens of *Umbra limi,* inhabiting a tributary of Chittenango Creek, near Bridgeport, New York, our three individuals of *G. cylindriformis* were taken on August 29, 1931.

Genus Dactylogyrus Diesing, 1850

Without designation of the species concerned, Hess (1928:138) has given the first records of the occurrence of the genus Dactylogyrus on the North American continent. In a preliminary abstract of his discovery, he recorded infestations on the gills of "small mouth and large mouth black bass, common sunfish, goldfish, carp and other fishes. As many as 1,600 flukes were taken from the gills of a fish 11 inches long, and 47 from a fish three-fourths of an inch long." In a later communication Hess (1930:136) has suggested that fishes may develop a partial or complete immunity to Dactylogyrus. In part, he based his argument upon the observation that the largest flukes of this genus are found on fishes that have become parasitized only recently, while individuals that have been parasitized for a year or more harbored very few flukes and even those were of smaller size than the ones found on recently infested fishes.

Hess (1930:136) has recommended potassium permanganate for the removal of Dactylogyrus from fishes under cultural and pond conditions, as discussed under the genus Gyrodactylus in this same paper. Members of the genus Dactylogyrus lay eggs instead of bringing forth viviparous young as do members of the genus Gyrodactylus. Since these eggs require several days for hatching, a single treatment of an infested pond is not as effective as for the viviparous Gyrodactylus. Hess (1930:135) has recommended that hydrated lime sufficient to cover the surface be sprinkled on the bottom of infested ponds when drained, for eggs and larvae protected by the mud are thereby destroyed.

In the literature, there are accounts of the occurrence of Dactylogyrus in the Eastern States (Maryland and New York), and records from as far west as Iowa. While no information is available as to the species concerned in these instances, it is highly probable that man has been an active agent in the distribution of Dactylogyrus on goldfishes as well as on other species disseminated in the interests of conservation and restocking of waters with game fishes from hatcheries.

The only record of the occurrence of Dactylogyrus in the Oneida Lake parasite survey is that given in Part II of this report (Mueller and Van Cleave, 1932) wherein *D. extensus* has been described as a new species.

Dactylogyrus extensus Mueller and Van Cleave, 1932

Host.—*Cyprinus carpio,* on gills.

This is the only species of Dactylogyrus which has been definitely recorded from North America. Two individuals of the carp (*Cyprinus carpio*), taken in June, 1931, from widely separated localities in Oneida Lake, bore specimens of *D. extensus* on the gills. See Part II for description.

Subfamily Tetraonchinae

The genera of this subfamily are so numerous, and so little work has been done to date upon the native representatives, that very little is known of the group in North America. Most of the existing references to members of the group in native waters use the generic name Ancyrocephalus, but there is evidence that many of the forms thus designated belong to other genera.

The history of the records of occurrence of Ancyrocephalus from North American hosts has been discussed in Part I of this report (Van Cleave and Mueller 1932:25), in connection with the original description of *Ancyrocephalus aculeatus.* Though the presence of the genus had been recorded previously for this continent by various authors, most of the earlier writers failed to make specific determinations for their material or determined their specimens as identical with species described for the European fauna.

There are records of this genus for several of the states from Iowa eastward to the Atlantic coast, and northward into Canada. In Oneida Lake we have encountered three species: *A. aculeatus, Tetraonchus monenteron,* and an unnamed species

(Pl. 28, Figs. 4-5) from *Ameiurus nebulosus* represented in our collection by two imperfect specimens. Each of the three species we have studied has been restricted to a single host species in each of three different families of fishes.

Ancyrocephalus aculeatus Van Cleave and Mueller, 1932*

Host.—*Stizostedion vitreum*, on gills.

The reader is referred to the original description of this species in Part I of the Oneida Lake parasite survey. All of the records of the occurrence of this worm in Oneida Lake are from the gills of *Stizostedion vitreum*, taken in the vicinity of Cleveland, N. Y. Following its discovery many specimens of *Perca flavescens* were examined for Ancyrocephalus, but with negative results.

From the gills of one infested pike perch forty worms were taken, but none was found on the skin or fins of the host.

Ancyrocephalus sp. ?

Plate 28, Figures 4–5

A single specimen of a bullhead (*Ameiurus nebulosus*) taken in Cleveland Harbor on June 24, 1931, served as host for four flukes of the genus Ancyrocephalus. All of the specimens were either damaged or lost in the handling. While the two defective specimens remaining in our collections are sufficient to demonstrate that the species is neither *T. monenteron* nor *A. aculeatus* they are insufficient to serve as the basis for an adequate description.

Tetraonchus monenteron (Wagener, 1857)

Plate 28, Figures 1–3

Host.—*Esox lucius*, on gills.

Although this worm has been placed in the genus Ancyrocephalus by certain authors, this position is erroneous. The worm constitutes the type of the genus Tetraonchus.

With characters of the genus. Small, about 0.85 mm. long. Head with two, or sometimes three pairs of papillae and two pairs of eyes. Intestine a single, unpaired, linear sac passing down middle of body. Vitellaria lateral, equivalent to intestine in longitudinal extent. Ovary and testis serially arranged, in close proximity, near center of body. Caudal attachment organ with four large hooks and sixteen marginal hooklets, of which two lie on the terminal, dorsal edge, two lie centrally at the anterior edge of the ventral surface, and on each side a pair of hooklets is found on the posterior lateral margin near the dorsal hooks. The remaining eight hooklets are grouped in two sets of four, one set occurring on either side of the ventral surface at the anterior lateral margins near the ventral hooks. The large hooks are much less curved than those of *A. aculeatus*. Muscle bands are developed inside the attachment organ for moving the large hooks, and

* This species was incorrectly described in certain features, in the original description, and it has since been ascertained that it does not belong in the genus Ancyrocephalus. See Part IV for a discussion of this worm.—Mueller.

a pair of strong muscle bands pass from the interior of the disc forward into the body of the worm.

Biology.—This parasite was originally described from *Esox lucius* of Europe and has never before been recorded from North America. So far as our records indicate, *T. monenteron* is specific for *Esox lucius* in Oneida Lake. Although the gills of *Esox niger* have been examined frequently the results have always been negative. Twenty or more specimens were found on the gills of each of four individuals of *E. lucius*.

According to the records of European investigators, this species is sharply restricted to *E. lucius* as a host on that continent also.

Trematoda: Order Digenea

Family Bucephalidae

The Bucephalidae are digenetic trematodes which depart from the usual concepts of trematode structure in that the anterior sucker is unrelated to the mouth opening. The simple rhabdocoel gut opens on the ventral surface of the body. This unique location of the mouth led Odhner (1905) to apply the descriptive name Gasterostomata to the suborder which includes the Bucephalidae and related genera.

Eckmann (1932) has divided the family into a number of genera as follows:

Key to the Genera of Bucephalidae

(* Denotes genera found in Oneida Lake.)

1 (a) A rhynchus at anterior end of body.................. **Prosorhynchus** Odhner, 1905
   (b) A sucker on anterior end of body.. 2
2 (a) Anterior sucker simple without accessory processes..**Bucephalopsis** Diesing, 1855*
   (b) Anterior sucker with a collar which is frequently provided with papillae......... 3
   (c) Fimbriae (tentacles) present in addition to anterior sucker....**Bucephalus** Baer, 1927*
3 (a) Ovary occurs at or anterior to the level of the forward testis; intestine sac-like .... **Rhipidocotyle** Diesing, 1858*
   (b) Ovary occurs between the testes; intestine sausage-shaped. **Dolichoenterum** Ozaki, 1924

Woodhead placed all the North American species in the single genus Bucephalus. But Baer, after a comparative study of the family places these species in three different genera as follows:

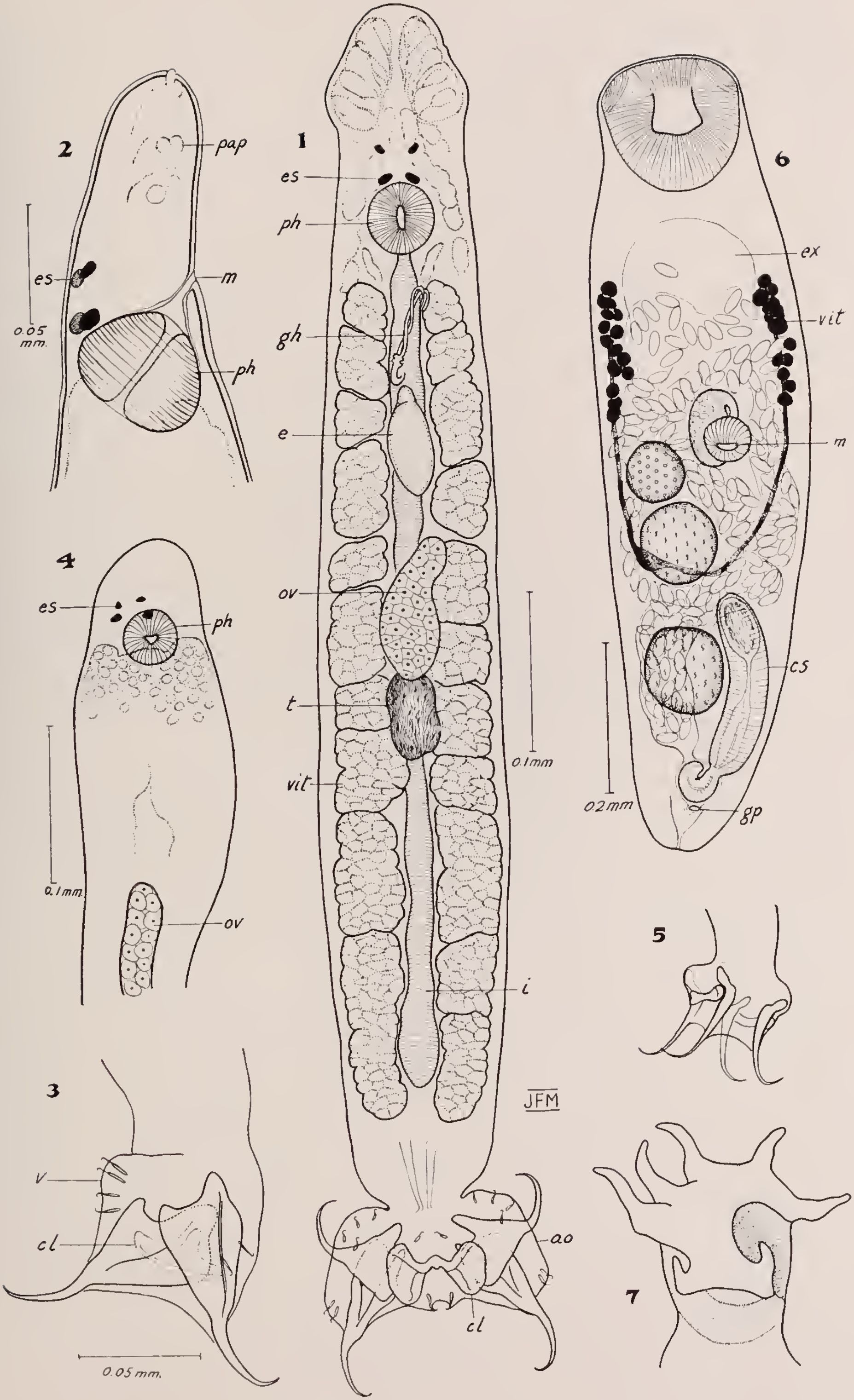
Bucephalopsis pusilla (Stafford 1905)
Rhipidocotyle papillosum (Woodhead 1929)
Bucephalus elegans Woodhead 1930

All of these species occur in Oneida Lake. Ceca and intestine of various predacious fishes serve as the habitat of these worms, and Woodhead (1929 and 1930) has maintained that each species exhibits rigid host limitations. The group has long been recognized as present in the North American fauna though in all the older literature the forms were put in the genus Gasterostomum. No satisfactory attempt at analysis of the species for North American hosts was made until Woodhead (1929 and 1930) published his two papers differentiating three distinct species.

Plate 28. Ancyrocephalus, Tetraonchus and Bucephalus. 1, *Tetraonchus monenteron*, ventral view of entire worm. 2, Head, lateral view. 3, Tail, lateral view. 4, *Ancyrocephalus* sp., from Ameiurus. View of body, from imperfect whole mount. 5, Three-quarter view of tail of *A.* sp. shown in Fig. 4 (scale as in Fig. 6). 6, *Bucephalus elegans,* ventral view. 7, Head of an older specimen (after Woodhead).

ao—attachment organ, cl—clamp, cs—cirrus sac, e—egg, es—eyespots, ex—excretory bladder, gh—genital hooks, gp—genital pore, i—intestine, m—mouth, ov—ovary, pap—cephalic papillae, ph—pharynx, t—testes, v—ventral surface, vit—vitellaria.

PLATE 28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Contrary to the conditions usually found in the digenetic trematodes, members of this family utilize mussels instead of snails as hosts for the cercariae. This fact has long been known and as early as 1899 Kelly recorded observations on the correlation between the occurrence of cercariae in Unionidae of the Illinois River and sterility of the female mussel.

In connection with this survey we have frequently encountered members of the Bucephalidae. One species, *B. pusilla,* is very readily distinguishable and, according to Woodhead's ideas of strict host specificity, the other two species, *B. elegans* and *R. papillosum,* are both likewise represented in our collections. The last two species are differentiated on the basis of the processes on the anterior sucker. However, although most of our specimens are sexually mature, as shown by the presence of numerous eggs, not one shows any well developed fimbriae or papillae. Therefore, since no morphological characters other than cephalic processes are available for differentiating *R. papillosum* and *B. elegans,* we have felt compelled to adopt the questionable policy of relying upon host relationships for the separation of these two species.

The host specificity of members of the Bucephalidae which Woodhead has maintained in his publications and in personal correspondence with the writers, is apparently supported by our collections. In every instance the worms in unusual hosts are immature. All bucephalids in our collections, from *Perca flavescens, Lepibema chrysops, Ameiurus nebulosus,* and *Esox niger,* are devoid of eggs and hence represent accidental introductions into hosts unsuited to bring the worms to maturity.

Bucephalopsis pusilla (Stafford, 1904)

Text Figure 1, Figures 1–3

Host.—*Stizostedion vitreum.* In ceca and intestine.

Bucephalopsis pusilla is the only member of the Bucephalidae which we have been able to recognize at all times in our collections. Our preserved specimens are slightly larger than measurements cited by Woodhead, for typical specimens are about 0.67 mm. long by 0.15 mm. wide.

In life, the worm is very active and the cephalic sucker is frequently shoved out at the tip of a slender neck. In this state specimens have much the appearance of small Alloglossidium.

The characteristic form of the sucker is well retained in fixed specimens.

Stizostedion vitreum is the only host in which we have found *B. pusilla* in Oneida Lake and conversely *B. pusilla* is the only bucephalid which we have found in Stizostedion, but it occurred in about 60 per cent of all pike perch which we examined. During the three months of June, July and August, when most of our collections were made, we found the worm in relative abundance in Stizostedion from both deep water and shore habitats.

While the life cycle is unknown, it is probable that one of the fresh-water mussels serves it as larval host, as has been demonstrated for the other two North American species. Mussels, especially those from deep waters, secured with the beam trawl, were examined and kept under observation for cercariae, but with negative results.

We have taken between four hundred and five hundred specimens of *B. pusilla* from a single host.

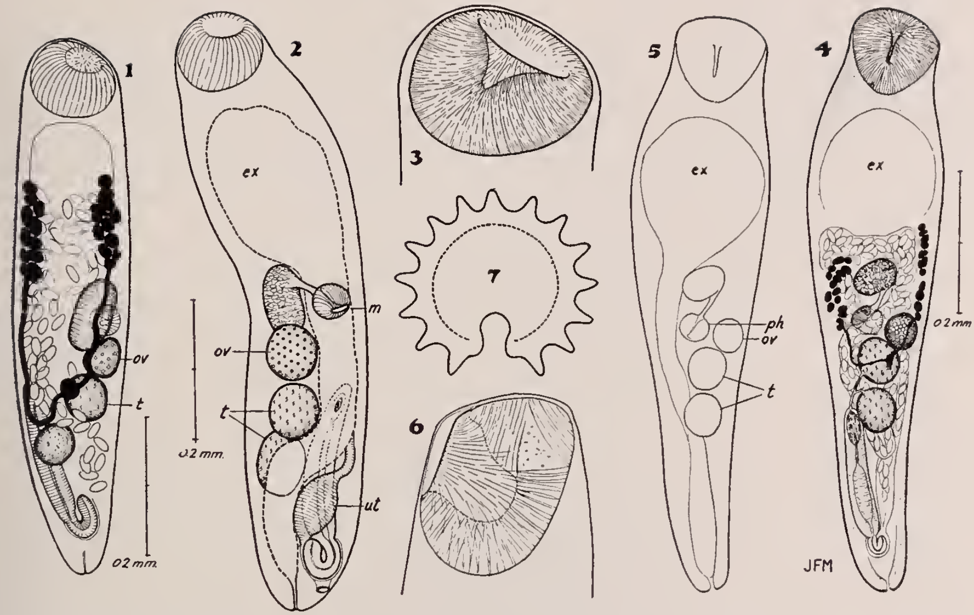


Fig. 1. Bucephalidae.

Bucephalopsis pusilla. 1, 2, Dorsal and ventral views of two individuals. 3, Lateral view of anterior sucker.

Rhipidocotyle papillosum. 4, Dorsal view of an individual. 5, Outline of same, showing extent of excretory bladder. 6, Lateral view of anterior sucker. 7, Anterior aspect of anterior sucker of an old individual (after Woodhead).

m—mouth, ov—ovary, ex—excretory bladder, t—testis, ut—uterus.

Bucephalus elegans Woodhead, 1930

Plate 28, Figures 6–7

Host.—*Ambloplites rupestris.* In ceca.

B. elegans is characterized by a crown of seven appendages, but these structures seem to be indicative of senescence. In our Oneida Lake collections some of the specimens from the rock bass show slight traces of seven papillae, but these never reach the proportions of fimbriae as figured by Woodhead (1930: Figs. 18 and 22). After careful and diligent search in both living and preserved specimens we have found only a few individuals on which even faint indications of seven cephalic papillae could be made out. However, in many instances we have observed two eminences at the antero-ventral corners of the sucker. The shape of the cephalic sucker in *B. elegans* is distinctly different from that of *B. pusilla,* but resembles that of *R. papillosum.* In both *B. elegans* and *R. papillosum* the opening of the sucker is directed ventrad. Dr. Woodhead has generously examined some of our specimens from the rock bass and has confirmed our determination of this material as *B. elegans.*

In the perch (*Perca flavescens*) we have found bucephalids in approximately 30 per cent of the individuals examined, and while not one of these bears eggs all seem to be clearly assignable to *B. elegans.* It is unusual to find such a high incidence of infestation in a host unable to bring the parasites to maturity.

In an exceptionally complete analysis of the life history of *B. elegans* (Woodhead, 1930:1), a small mussel, *Eurynia iris*, has been found to serve as intermediate host into which the miracidia penetrate. The sporocyst and cercaria generations develop in this same host. After leaving the mussel, cercariae penetrate into the skin and fins of fishes, there becoming encysted. Woodhead (1930:10) has performed feeding experiments to demonstrate the fact that these encysted cercariae complete their development when the fish bearing them is eaten by another fish suitable to serve as host.

Rhipidocotyle papillosum (Woodhead, 1929)

Text Figure 1, Figures 4–7

Hosts.—*Micropterus dolomieu* and *Micropterus salmoides*. In digestive tract.

As characterized by Woodhead (1929:259), *R. papillosum* is distinguishable from *B. elegans* on the basis of a single morphological character, the fact that in late maturity *R. papillosum* bears fifteen cephalic papillae while *B. elegans* bears but seven. Other characteristic differences such as relative size of body, size of eggs, and relative size of the digestive tract are unavailable for differentiation of our specimens because of complete overlapping of size ranges in material before us. We have concluded that specimens from both species of the black bass in Oneida Lake are referable to *R. papillosum*, basing our determination in large measure upon the claims of host limitations set forth by Woodhead in his publications and emphasized in private communications. We have never seen any indication of cephalic papillae or fimbriae on our bucephalids from black bass, but specimens submitted to Woodhead were kindly verified as to determination.

Esox lucius has been recorded as a host of *R. papillosum*, but not one of the nineteen specimens of this fish which we have examined from Oneida Lake has borne this species. Possibly this is explainable on the ground that all of our records involve pike twelve inches or more in length, whereas the infestation records of Woodhead concerned "small specimens".

Woodhead (1929:270) has traced the development of *R. papillosum*, having determined that the cercariae are developed in *Elliptio dilatatus*, a fresh-water mussel. These cercariae after leaving the mussel actively penetrate the skin of fishes, becoming encysted usually at the base of the fin rays. Here the cyst remains until the host is eaten by a larger fish, within whose digestive tract the Bucephalus is liberated. Functional maturity is attained only by those flukes which find themselves in suitable hosts. Both species of black bass carry this worm frequently, but the number per fish is low, usually not more than six to ten but occasionally more.

Sterile bucephalids.—Bucephalids which we have found in *Perca flavescens*, *Esox niger*, *Ameiurus nebulosus*, and in *Lepibema chrysops*, are all immature though the body is well developed, with complete internal organization, and conspicuous gonads, but totally devoid of uterine eggs. We are relegating these immature bucephalids, except those from Perca, to an unresolved group of *elegans-papillosus*. Those from the perch are apparently *B. elegans* (see above).

Family Gorgoderidae

The Gorgoderidae represent a fairly homogeneous family of digenetic trematodes which reach sexual maturity in the urinary bladder and ducts of fishes and amphibians. In the fishes of Oneida Lake the only genus representing this family is Phyllodistomum, which dwells in the urinary bladder of various fishes.

Genus Phyllodistomum Braun, 1899

The phyllodistomes are very much flattened trematodes with the body usually divided into a narrow forebody bearing the oral sucker at its anterior end, and a much expanded, leaf-like hindbody bearing most of the genitalia. Acetabulum near the union of the two divisions. Suckers small but powerful. Vitellaria a single pair of undivided or lobate glands posterior to the acetabulum. Ovary lateral, posterior to vitellaria. Testes oblique. Uterus forming wide loops through the hindbody. Genital pore median between fork of crura and acetabulum.

In 1903 Osborn published the first record of a member of this genus for the American continent when he described *P. americanum* from the urinary bladder of a salamander. The following year (1904) Stafford recorded two species from fresh-water fishes. His work stood practically unsupported by additional records until Pearse (1924:152) showed that Stafford had confused two species under his concept of *P. superbum.* In rectifying this error, Pearse named the salvaged species *P. staffordi* and in the same paper described still another species as *P. fausti.* Holl in 1929 described two additional species, *P. pearsei* and *P. carolini,* bringing the total to seven species of the genus recognized from North America. An eighth species was added by Loewen (1929) who apparently misinterpreted the genus Phyllodistomum and described a new species of that genus under the name *Catoptroides lacustri.* Thus seven species of the genus Phyllodistomum are found in North American fishes. We have found three of these seven species in the fishes of Oneida Lake.

With regard to distribution on this continent, members of the genus Phyllodistomum show great irregularity, as pointed out by Holl (1925:51). *P. staffordi* seems not restricted to any given area or drainage but is general in Ameiurus. *P. superbum* occurs commonly in perch of the Great Lakes and St. Lawrence drainage, hence our Oneida Lake records conform to the general range of the species. Most of the remaining phyllodistomes are too imperfectly known to warrant predictions as to range. *P. pearsei* and *P. carolini* have been recorded from North Carolina only; until our present records from Oneida Lake, *P. lacustri* and *P. fausti* have been recorded from the Mississippi drainage only.

In the following key, in part adapted from Holl (1929), all the members of this genus recorded for North America are differentiated.

Key to the Species of Phyllodistomum Reported From North America

(An asterisk denotes those species recorded from Oneida Lake.)

1 (a) Adults in urinary bladder of amphibians. Anterior region of body not sharply set off from a broader posterior region. Vitellaria distinctly three-lobed .... **P. americanum** Osborn

(b) Adults in urinary bladder of fishes. Anterior region of body sharply set off from a broader posterior region. Vitellaria not distinctly three-lobed 2

2 (a) Vitellaria lobate 3
(b) Vitellaria pyriform 5
3 (a) A distinct groove or at least a sharp lateral angle on each side of the base of the neck marks the union of broad posterior expansion with narrow anterior region ....**P. staffordi** Pearse*
(b) No distinct groove or notches between body regions........................ 4
4 (a) Hindbody with lateral margins finely dentate........................**P. carolini** Holl
(b) Hindbody with lateral margin sagittate, each tooth apparently muscular **P. lacustri** (Loewen)
5 (a) Oral sucker larger than acetabulum; intestine extends nearly to posterior margin ....**P. pearsei** Holl*
(b) Oral sucker not larger than acetabulum.................................. 6
6 (a) Body margin not crinkled. Notch at posterior end ....**P. folium** (v. Olf.)
(b) Body margins more or less crinkled.. 7
7 (a) Distinct median posterior notch. Postacetabular region widest just behind acetabulum. Testes somewhat separated................................**P. superbum** Stafford*
(b) No distinct notch at posterior end. Postacetabular region widest in middle. Testes close together ....**P. fausti** Pearse

Phyllodistomum superbum Stafford, 1904

Plate 29, Figures 1–4

Hosts.—*Perca flavescens* and *Stizostedion vitreum:* in urinary bladder.

This is by far the most abundant species of Phyllodistomum in Oneida Lake, considering its high incidence of infestation and the abundance in individual hosts. The worm is orange or ruddy in life. In living specimens the margin is smooth but the edge of the body is thrown into a series of ruffles or undulations, commonly three on each lateral margin. Young individuals show little differentiation of fore- and hindbody, and in the smallest examples which we have taken from the urinary bladder the sides of the body expand very evenly from the oral sucker to a point a short distance from the posterior extremity. Specimens of *P. superbum* from the pike perch are on the average larger than those from the yellow perch and show a greater development of the marginal undulations, but there are no significant differences between the two forms.

We estimate from our records that 90 per cent or more of the adult pike perch in Oneida Lake carry *P. superbum* in the urinary bladder. Twenty to twenty-five worms were often taken from a single fish, but lesser numbers were the usual occurrence. Approximately 40 per cent of the yellow perch in Oneida Lake harbor *P. superbum* in the urinary bladder, the severity of individual infestations varying from single worms to more than 30 in one bladder. The yellow perch must play a very important role in the life of this parasite and the life of the lake as a whole. Considering the fact that the yellow perch is probably the most abundant food fish in Oneida Lake and is found in practically all situations, a 40 per cent infestation with phyllodistomes would indicate a tremendous population of this worm in the lake.

The type of habitat from which fish are taken apparently has little to do with the incidence of this parasite for it is generally distributed throughout the lake. *P. superbum* is not seasonal in its occurrence for it is present throughout the summer months, and perch taken in December, January and February carried considerable numbers.

Unusual Host Records.—Four species of fish, in addition to the normal hosts discussed in the foregoing paragraphs, have given us specimens of *P. superbum.* The brown trout (*Salmo fario*) was the only one of these having *P. superbum* in the urinary bladder, for the other fishes (*Esox lucius, Percina caprodes zebra,* and *Percopsis omisco-maycus*) held specimens in the digestive tract that were clearly ectopic.

Of sixteen individuals of brown trout which appear in our records, only one contained *P. superbum.* This was a fifteen-inch specimen taken by gill net in Cleveland Harbor on June 18, 1931 (host record 580). Six worms were taken from the urinary bladder, and though these were mature they were small and apparently not in good condition. Apparently the brown trout is not a normal host of *P. superbum.*

Two worms secured after teasing the bodies of six specimens of *Percina caprodes zebra* were entirely normal and might represent a case of normal infestation.

Phyllodistomum staffordi Pearse, 1924

Plate 29, Figure 6

Host.—*Ameiurus nebulosus,* in urinary bladder.

Large and conspicuous, with white or creamy color in life. Narrow, tapering forebody and flat, discoidal hindbody, which lacks ruffled margins and posterior notch. The distinct groove separating the forebody from hindbody, which Holl (1929:51) has emphasized as diagnostic for *P. staffordi,* is not always observable in our specimens, but there is a sharp lateral angle at the base of the neck, which we have interpreted as indicative of the groove mentioned by Holl.

Acetabulum larger than oral sucker. Vitellaria, ovary, and testes lobed. Coils of uterus in one plane, evenly distributed through the disc, with extensive coils between the testes and extending laterally beyond the crura to near the margins of the disc. Crura dorsal to uterine coils, broad and roughly parallel to lateral margins of disc, passing to near posterior end of body.

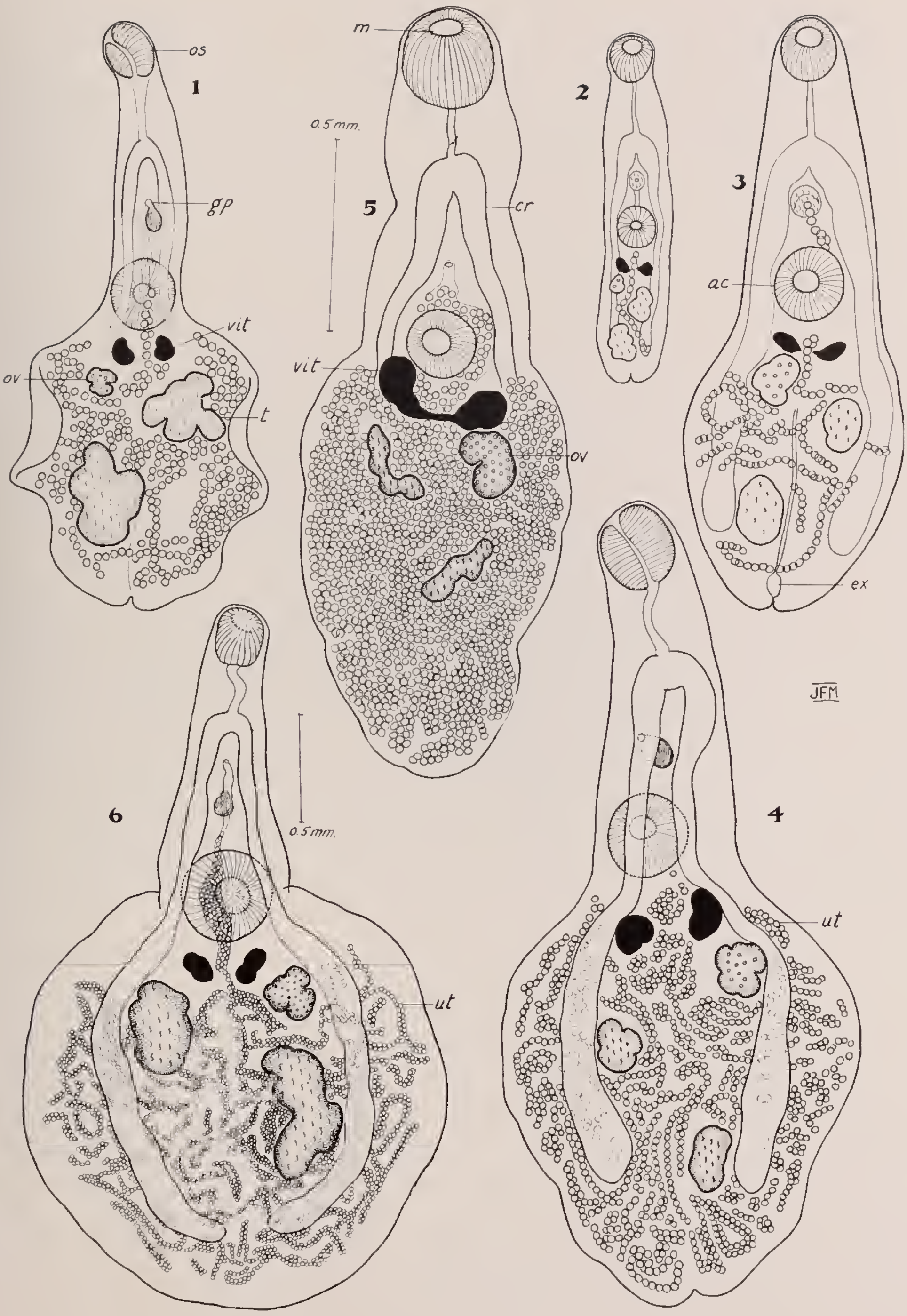
Our collections contain 20 specimens of *P. staffordi* from a total of 56 specimens of *A. nebulosus.* Apparently not more than 10 per cent of the mature common bullheads in Oneida Lake carry *P. staffordi.* Individual infestations are very light, one or two worms in a bladder, with seven as a maximum. It is probable that *P. staffordi* is generally distributed in Oneida Lake in all habitats supporting *Ameiurus nebulosus,* but that it does not occur in all tributary waters is indicated by the fact that all specimens of the common bullhead from the Cleveland mill pond were negative for *P. staffordi,* while individuals of the same species in Cleveland Harbor only a few hundred feet distant carried the worm.

P. carolini Holl and *P. lacustri* (Loewen) were not found in any of the catfishes of Oneida Lake. *P. carolini* is known from *Ameiurus natalis* from North Carolina only, while the only records available for *P. lacustri* are from *Ictalurus punctatus* of the Mississippi River.

Plate 29. The Genus Phyllodistomum. (The scale with Fig. 5 applies to Figs. 1–5). 1, *P. superbum,* dorsal view of a specimen from *S. vitreum* showing crinkled margins of the hindbody characteristic during life. Figs. 2, 3, 4, *P. superbum,* various growth stages from the yellow perch. 5, *P. pearsei* from the large-mouth bass, ventral view. 6, *P. staffordi,* dorsal view of specimen from *A. nebulosus.*

ac—acetabulum, cr—crura, ex—excretory bladder, gp—genital pore, m—mouth, os—oral sucker, ov—ovary, t—testes, ut—uterus, vit—vitellaria.

PLATE 29



Phyllodistomum pearsei Holl, 1929

Plate 29, Figure 5

Host.—*Micropterus salmoides;* in urinary bladder (?)

Phyllodistomum pearsei was originally described from the urinary bladder of a sunfish (*Enneacanthus gloriosus*) in North Carolina. We have a single specimen from the large mouth black bass, which we have assigned to this species. The worm was discovered in the water at the bottom of the dissecting pan after autopsy of a bass. There can be no doubt as to the worm having come from the bass, but specific location in the host remains uncertain. While it is highly probable that the urinary bladder was its place of residence there is the possibility that the worm had been an ectopic resident of the digestive tract, after liberation from the urinary bladder of some food fish. A single host (*Enneacanthus gloriosus*) has been recorded for this species, and since this fish is not found in the Oneida Lake area the local host must in all probability be some other member of the sunfish family. Either the bass or some one of the local sunfishes could fulfill the role of host. Repeated examinations of black bass, representing both species, and of the common sunfish have failed to supplement this single accidental discovery of *P. pearsei* in the Oneida Lake area. The fish from which *P. pearsei* was recorded was eight inches in length and was taken in Fairchild Bay on July 18, 1929.

Family Plagiorchiidae

It has been shown under the discussion of the Allocreadiidae that a number of genera of fish trematodes previously placed in the Plagiorchiidae do not rightly belong in this family. However, the genus Vietosoma, described by us in Part I, appears to constitute a legitimate representative of this family finding a location under the subfamily Reniferinae. The Reniferinae are characterized by crura of medium length, with uterine coils or an open space intervening between the tips of the crura and the posterior extremity of the body. The seminal receptacle is lacking, and the testes symmetrical, lateral. This subfamily comprises parasites of the lungs, trachea, and esophagus of snakes, but Vietosoma seems to constitute an exception in its host relationships.

Genus Vietosoma Van Cleave and Mueller, 1932

Small, compact, seed-shaped trematodes, with spinose skin. Genital pore median, cirrus sac present. Ovary with many marginal lobes, flattened, dorsal, just above acetabulum. Laurer's canal present. Seminal receptacle lacking. Testes lateral, symmetrical, internal to crura. Crura extend to within short distance of posterior tip. Coils of uterus intercrural, and posterior to crural tips. Vitellaria lateral, extracrural, from pharynx to crural extremities. Excretory bladder a long median unbranched stem extending from pore anteriad between testes to posterior border of ootype complex; anterior end of bladder square, or with very slight indication of forking. In as much as the excretory bladder is not plainly Y-shaped the genus fails to coincide perfectly with the characters of the Plagiorchiidae, but in other respects its organization seems to ally it definitely with this family. Among the Reniferinae it appears to stand closest to the genus Pneumatophilus.

Vietosoma parvum Van Cleave and Mueller, 1932*

Host.—*Ictalurus punctatus.* In intestine and stomach.

This species was transferred to the Heterophyidae in Part II on the basis of a superficial resemblance to the heterophyid genus Euryhelmis. Later detailed study by Mueller (1933) showed that the worm did not fit into this group, and it was restored to the position originally assigned to it. This unfortunate shifting around was due in part to the small size of the worm and the consequent difficulty of study and interpretation. The species represents the only true member of the Plagiorchiidae occurring in American fresh-water fishes.

The three specimens of the channel catfish which we have examined bore mass infestations of *Vietosoma parvum.* In addition, a single immature specimen was encountered in the parasite population of a bullhead (*Ameiurus nebulosus*) out of the total of 82 common bullheads examined. This would indicate that this single worm in the bullhead represents an accidental introduction devoid of significance. The channel catfish is the sole vertebrate of importance in the life cycle of Vietosoma in Oneida Lake. The extent of infestation in Ictalurus could not be determined, for though this fish is relatively common in the lake we were unsuccessful in taking it in the gear at our disposal. Catfish were occasionally taken by commercial carp seiners. Large scale fishing operations for the eradication of carp have proved so unprofitable in this lake in recent years that activity along that line has been curtailed. In consequence the incidental catch of channel catfish has been much reduced. The three fruitful specimens serving as host to Vietosoma were secured from a commercial fisherman operating in Fisher's Bay. The life cycle remains unknown.

Family Allocreadiidae

As conceived by Fuhrmann (1928:105) and by Poche (1926:159) the family Allocreadiidae is relatively restricted. Both of these authors exclude a number of genera which to the present writers seem to show characters wholly compatible with those of other genera commonly accorded a place in the family. As viewed by the two authorities cited, the genus Bunodera is recognized as type of a family Bunoderidae. As pointed out later in this same section, we can see no basis for such a separation and hence we return Bunodera to the Allocreadiidae where it stands close to its companion genus Crepidostomum.

In like manner the genus Lissorchis has been generally admitted as representing a distinct family, but after a comparative study of Triganodistomum and Macroderoides we have come to the conclusion that there is no adequate basis on which to differentiate these genera from the Allocreadiidae.

The major evidences leading to the foregoing conclusions are set forth in the following paragraphs.

When Pearse (1924) founded the genus Macroderoides, he assigned it to the family Plagiorchiidae. This position was accepted by the present writers in Part I of this series of reports, when *M. flavus* was added to the genus. More recently we have been giving particular attention to the so-called plagiorchids of fishes and

* For a detailed study of this species see Part IV.

have arrived at some conclusions which seem to demand a reconsideration of this group. All of the current diagnoses of the Plagiorchiidae specify the possession of a Y-shaped excretory bladder for members of this family. In Macroderoides, Lissorchis, Triganodistomum, and those species from North American fishes which have been ascribed to Plagiorchis, the bladder is a simple sac or tube without bifurcation.

On the above grounds the species from fishes assigned by American writers to the genus Plagiorchis must be removed from the Plagiorchiidae. Simer's generic name Alloglossidium becomes available for the species from fishes misplaced in the genus Plagiorchis. Alloglossidium, Plagiocirrus, and Plagioporus, stand close together in the family Allocreadiidae. Triganodistomum and Macroderoides converge toward Alloglossidium and through it find relationship with the Allocreadiidae also. The work of Dollfus (1930:143) provides conclusive evidence for the removal of the so-called plagiorchids of American fishes from the Plagiorchiidae to the Allocreadiidae.

Family Diagnosis.—As thus composed the family Allocreadiidae is based upon the following characters. Small to median distomes, of oval or elongate form, and only moderately robust in structure. Two suckers of approximately equal size, the ventral sucker anterior to middle of body. Ovary behind acetabulum, usually anterior to testes. Testes either serial or oblique. Uterus behind acetabulum, and of varying posterior extent. Laurer's canal present. Seminal receptacle present except in some marine forms. Vitellaria follicular in lateral zones, at times converging at posterior end. Genital pore either in front of acetabulum, on median line, or laterally displaced toward the left margin, not farther back than middle of acetabulum. Cirrus sac present, with ample vesicula seminalis. Excretory bladder sac-like or tubular. Eggs relatively large.

The previously mentioned genera which we bring together in this family fall into four natural groups. One of these is made up of Bunodera and Crepidostomum. The chief distinguishing character of this group is the development of six muscular papillae upon the oral sucker.

The second group is characterized by a lateral genital pore, and includes the genera Lissorchis, Plagioporus, Plagiocirrus, and Triganodistomum.

The third group is characterized by simple suckers and median genital pores; the uterus extends to the posterior end. This group comprises the genera Alloglossidium and Macroderoides.

The fourth group is characterized by simple suckers and median genital pore, but the uterus is restricted to the small space between the acetabulum and the anterior testis. The genus Allocreadium belongs here.

Genus Allocreadium Looss, 1900

The only representative of the genus Allocreadium which we have found belongs to a species described as new in Part II of this series of reports. The genus is very sparsely represented in Oneida Lake.

Allocreadium ictaluri Pearse, 1924

Synonym: *Allocreadium halli* Mueller and Van Cleave, 1932

Host.—*Ameiurus nebulosus,* in intestines.

For a description of this species see Part II of this report. On June 25 and 30, 1931, we took specimens of the common bullhead from Cleveland Harbor, which were lightly infested with *A. halli,* one of the bullheads containing but a single specimen. Both fish were taken in shallow water with mud bottom. Nothing is known of the life cycle of *A. halli.* Since our original description, further information indicates that this species is probably a synonym of *A. ictaluri* Pearse. Our original comparisons were made on the basis of Pearse's figure. It now appears that Pearse's species was very poorly illustrated. The type of *A. ictaluri* has subsequently been examined by us and found to resemble *A. halli* more closely than it does Pearse's figure of *A. ictaluri.*

Genus Crepidostomum Braun, 1900

The genus Crepidostomum, as represented in the North American fauna is still very imperfectly understood. In a manuscript thesis, S. H. Hopkins, of the University of Illinois, has shown that Acrolichanus is not a valid genus and has placed *A. lintoni* in the genus Crepidostomum. In this same thesis Hopkins recognizes *C. farionis* as a circumboreal species whose distribution is limited by the presence of salmonid fishes and invertebrates suitable to serve as hosts. Hopkins recognizes six distinctively American members of the genus, two of which seem to the present authors lacking in morphological characters sufficient to warrant separation. *C. isostomum* Hopkins seems to differ from *C. canadense* Hopkins in a degree that does not transgress the bounds of individual variation. Consequently, the present writers believe that *C. isostomum* and the circumboreal species *C. farionis* are the only forms in North America with genital pore anterior to the crural fork. Regarding *C. vitellobum* which Faust differentiated from *C. farionis,* Hopkins has re-examined some of the type material and has pronounced the former a synonym of *C. farionis.*

In a very recent publication Hunter and Bangham (1932:145) have described *Crepidostomum hiodontis* as a new species which they believe to be distinguishable from *C. illinoiense* Faust, 1918. The points which they have cited as available for differentiating the two species are in part due to misstatements in the original description of *C. illinoiense* and in part to a lack of appreciation of the extent to which individual variation may go in this genus. Hunter and Bangham state that in *C. hiodontis* the acetabulum is slightly larger than the oral sucker, while in *C. illinoiense* the oral sucker is the larger. It is evident that Faust (1918:191) included the papillae in his measurements of the oral sucker, for his drawing (1918, Fig. 16) depicts an acetabulum distinctly wider than the oral sucker. As additional points of distinction, Hunter and Bangham (1932:148) mention the relative length of the cirrus sac and the relative number of eggs in the uterus. Studies on other species of Crepidostomum, especially of *C. cooperi,* have forced the present writers (Van Cleave and Mueller, 1932) to consider both of these points highly variable within the species and unavailable for specific diagnosis except when accompanied by less variable characters. Furthermore, specimens of *C. illinoiense* from the type locality have been examined and found to be in complete agreement with the description of *C. hiodontis*. In consequence, the present writers maintain that *C. hiodontis* is a direct, unqualified synonym of *C. illinoiense*.

Hunninen and Hunter (1933) have described from trout two species of Crepidostomum, *C. fausti* and *C. transmarinum*. In this paper the authors set forth that *C. farionis* is a European species, and that the American form from trout, hitherto called by this name, is distinct, and for this they retain the name first applied by Nicoll, *C. transmarinum*. *C. fausti* is a new species made by these authors, and is said to be smaller than *C. transmarinum*. The authors regard the sexual maturity of the smaller form as convincing evidence of the distinctness of the two forms. But when it is remembered that certain species of Crepidostomum begin to produce eggs while still in the intermediate host such evidence appears inconclusive. The other characters given for separation of the two forms appear of dubious value, compared with the variations we have observed in *C. cornutum* and *C. cooperi*. We doubt the validity of separating these forms from *C. farionis*.

As conceived by the present writers, seven species of Crepidostomum deserve recognition in the North American fauna: *C. cornutum, C. cooperi, C. isostomum, C. ictaluri, C. farionis, C. illinoiense,* and *C. lintoni*. Of these the first four are found in the Oneida Lake fauna.

Crepidostomum cornutum Osborn, 1903

Text Figure 2, Figures 1–6

Hosts.—*Ambloplites rupestris, Micropterus salmoides, Ameiurus nebulosus, A. natalis, Eupomotis gibbosus;* in digestive tract.

This is the most abundantly represented species of Crepidostomum in Oneida Lake. It is so highly variable that the differences between the extremes of variation would be sufficient for the recognition of several species were it not for the presence of intermediate forms.

In *C. cornutum* the body is usually broad and flat. Length four to six times the width. Outline oblong, sides straight and parallel, head rather square in front, tail bluntly rounded. Acetabulum smaller than oral sucker. Pharynx only about one-fifth the diameter of this latter organ. Lateral papillae large and prominent, forming widest part of the body. Any or all of these characters may be altered in unusual specimens. Hopkins (1931:87), in his key, uses the length of the dorsal papillae to separate *C. ambloplitis* and *C. cornutum*. This character can not be relied upon to separate species of Crepidostomum. The length of the oral papillae varies greatly with the state of contraction, and in any case, whether or not they extend past the anterior margin of the oral sucker depends largely upon the degree to which the oral sucker is tilted, a matter of accident entirely. As proof of this we can add that of our many specimens of *C. cornutum* not one in ten shows the dorsal papillae anterior to the oral sucker.

The size of the suckers varies with the size of the worm. In the smaller mature worms the oral sucker, measured inside the lateral horns, is about 0.210 mm. in diameter. In one of the larger worms the corresponding measurement is about 0.450 mm. The cirrus sac is long and slender and makes a sigmoidal curve.

It usually curves to one side of the acetabulum, and posterior to this makes a complete curve in the reverse direction. The eggs in our specimens are variable. In smaller individuals the eggs measure 0.060 mm. in length; in larger ones, 0.090 mm. The width of the eggs is approximately two-thirds of the length or less. Between these two extremes we find a complete transition of eggs with intermediate dimensions apparently correlated with the size of the worm.

In life, these worms are vigorously active, white or colorless, and some individuals appear much more rugged and opaque than others. However, we were unable to find any diagnostic differences between the two kinds. Most of our worms are small—about 1.0 to 1.5 mm. in length, but we have about six specimens of large size, measuring from 2.5 to 3.0 mm.

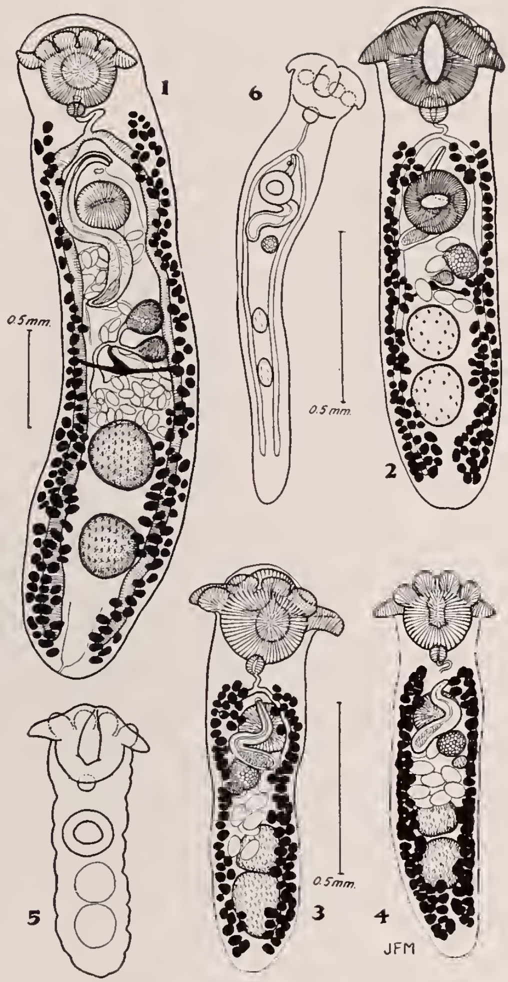


Fig. 2. *Crepidostomum cornutum.* 1, Large individual from the rock bass, dorsal view. 2, An average sized worm from a rock bass. 3, Specimen from *M. dolomieu.* 4, Specimen from *M. salmoides.* 5, Specimen from *A. nebulosus.* 6, Abnormal specimen from the sunfish. (Figures 2–6 drawn to same scale as that shown with 3 and 6.)

The rock bass carried *C. cornutum* in greater abundance and more often than did any other host in Oneida Lake, and we regard it as the natural host of the worm here. Our specimens from this host number about 1200. These worms range from 1 to 3 mm. in length, with width in proportion, and show differences in the density of the body, number of eggs, etc. The largest worms have the organs well separated and their course well outlined against the clear background of the rest of the body. The smaller worms have the organs more compactly massed together, giving a dense, solid appearance.

Apparently infestation with *C. cornutum* in the rock bass is correlated with the habitat of the vertebrate and invertebrate hosts. The infestation abounds in the deep or open-water fishes, and is lacking in fishes of the shallow, protected, shoreline habitats.

Our next largest collection of *C. cornutum* is from the small mouth black bass. In both the rock bass and the small mouth bass the heavy infestations were invariably found in fish taken from gravel bottom areas, which are doubtless more favorable than mud bottom areas for the crayfish essential in the life cycle of *C. cornutum*.

Although we examined 38 large mouth bass from numerous points around the lake shore we found a total of but six specimens of Crepidostomum, all belonging to the species *C. cornutum*. *M. salmoides* is a fish of the sheltered situations with shallow water and muddy bottom. It has been shown in the case of the rock bass and small mouth bass that this habitat does not favor infestation with *C. cornutum*. We therefore regard the habitat preference of the large mouth bass as explanatory of its freedom from this parasite.

We have about ten typical *C. cornutum* from the yellow bullhead, taken from two fish caught near Cleveland, but the yellow bullhead cannot be regarded as an important host, in Oneida Lake.

About ten specimens from *A. nebulosus* do not appear normal, and in one case monorchism was observed. Apparently this host is unfavorable.

A number of Crepidostomum taken from nine sunfish in July, August and September, from habitats mainly at the western end of the lake, are of uniform appearance and differ from any other Crepidostomum we have in being very much emaciated, so that the suckers bulge from the body. They are all immature. Some contain a few eggs, but this cannot be regarded as indicating normal maturity since Crepidostomum often is precocious in the crayfish, from which worms are frequently taken bearing eggs in the uterus. Hopkins (1931) restudied six specimens of Crepidostomum from the sunfish in Cooper's collection. He notes they are all immature and poorly preserved, and concludes that they "cannot be assigned to any known species". On the general basis of size and proportion of suckers these worms in our collection have been determined as *C. cornutum* which have failed to develop normally because of entrance into an unsuitable host. Since we have never found any mature worms anywhere resembling this form exactly, we think it necessary to identify the worms as stunted individuals of *C. cornutum*, modified by residence in an abnormal host. Infestation of sunfish with these worms is about 25 per cent. The number found in any one fish varied from four to fifty, but all were immature and abnormal. No other species of Crepidostomum is found in the sunfish in Oneida Lake.

We may summarize the facts for *C. cornutum* in Oneida Lake as follows. It is found in heavy infestations in its potential hosts when these frequent fairly deep open water with gravel bottom. It is lacking from its normal hosts when these dwell on mud bottom or in shallow water. Its important definitive hosts are (in correlation with the above) *M. dolomieu* and *A. rupestris*. It has as potential definitive hosts *M. salmoides* and *Ameiurus natalis*, in which it appears to develop normally, but in these hosts habitat preferences do not permit general infestation. Finally *Ameiurus nebulosus* and *Eupomotis gibbosus* may also harbor the worm occasionally, but both of these hosts are unfavorable to normal development.

Crepidostomum cooperi Hopkins, 1931

Synonyms: *C. solidum* Van Cleave and Mueller, 1932; *C. ambloplitis* Hopkins, 1931

Hosts.—*Perca flavescens;* and as accidental (?) parasite in *Leucichthys artedi tullibee, Ameiurus nebulosus, Notemigonus crysoleucas, Cyprinus carpio,* and *Necturus maculosus.* In digestive tract.

In Part I of this report (Van Cleave and Mueller, 1932:32) this species was described under the name *Crepidostomum solidum.* While that description was in press, Hopkins (1931) described the same species under the name *C. cooperi,* and the present writers made acknowledgment of the synonymy in a footnote appended to the original description of *C. solidum.* In the same note it was set forth that *C. ambloplitis* of Hopkins is also a direct synonym of *C. cooperi. Perca flavescens* seems to be the only normal vertebrate host of *C. cooperi* in Oneida Lake. In each of the other hosts recorded for this species there is but a single instance of its occurrence in our records.

These worms are small, the largest not more than 1.3 mm. in length. Widest diameter at level of acetabulum. A perceptible constriction or neck behind oral sucker. Posteriorly the body tapers to a point. Oral sucker proportionately smaller than in *C. cornutum,* its papillae less conspicuous. Lateral papillae blunt, short, and recurved. The body shape is the most easily recognizable feature, but unfortunately not always constant. Oral sucker and acetabulum of approximately the same size, pharynx equal in length to one-third or more of the diameter of oral sucker. Genital pore between acetabulum and crural fork. Uterus between first testis and acetabulum, and contains only a few relatively large eggs—about .060 x .040 mm. in diameter.

We have records of sixty-nine perch infested with *Crepidostomum cooperi.* The worms from thirty-nine of these were kept and mounted, and constitute our material of this species. The worms from the other thirty specimens were identified at sight and then discarded. Our specimens show all variations in appearance from the "*ambloplitis*" to the "*cooperi*" form of Hopkins. We also found as an additional variation in this species a form which has the body inflated and the cirrus sac enormously enlarged. We illustrated these variations in our description of *C. solidum.*

We have all of these varieties from the perch and it seems impossible to correlate a particular body form with the season or other external factors. Collections of Crepidostomum from individual fish often show the presence of all of these types together in the same host. The commonest form is that figured by Hopkins as "*C. ambloplitis*". The form next in abundance is the "*C. cooperi*" type of Hopkins, and type of the species. The form with the enormous cirrus sac is uncommon, and evidently Hopkins did not encounter it.

Our material from the tullibee consists of only four worms—all small and of the "*ambloplitis*" type. The single worm from Ameiurus is in the same category.

Four worms from a single golden shiner are all of the type with the large cirrus sac, as are also three worms from a carp.

It appears that infestation with *C. cooperi* in the perch cannot be closely correlated with habitat, but is pretty generally distributed among the perch in the lake. Infestation is usually very slight, the incidence roughly about 25 per cent. In this respect *C. cooperi* differs sharply from *C. cornutum* which was strictly correlated with habitat. We have records of the infestation at all seasons, fish taken through the ice harboring some of the best developed specimens of the worm.

Seventy young perch, about two inches in length, caught with the trawl in deep water off Cleveland, contained no Crepidostomum. They were still feeding on plankton, which no doubt accounts for the absence of infestation, which sets in when they begin to eat larger food.

The perch is evidently the normal host of this worm in Oneida Lake. From the figures of the occurrence in other hosts given above it will be seen that these hosts play a small part in its biology. We have no records of it at all in the rock bass, from which Cooper got some of his specimens.

In an unpublished dissertation for the doctorate in the Library of the University of Illinois, S. H. Hopkins has set forth a very complete picture of the life cycle of *C. cooperi*. The intrauterine eggs are never embryonated. The miracidium has been observed. Rediae develop in the gills and mantle of *Musculium transversum*, a small bivalve mollusc belonging to the Sphaeriidae. The rediae migrate from the gills and mantle to the liver of this bivalve, and here the cercariae are developed. After the cercariae leave the liver of the bivalve they enter the bodies of mayfly nymphs and here as metacercariae become encysted in the muscles and body cavity.

Within the mayfly the metacercaria does not continue to grow as does the larva of *C. cornutum* in the body of the crayfish. However, the gonads of the minute metacercaria do continue to grow, thus becoming relatively larger in older cysts than in younger larvae. Hopkins has offered this as a plausible explanation for the highly variable appearance of the gonads in individual adult worms found in fishes. A recently encysted metacercaria taken into the gut of a fish would have relatively small gonads, while an older cyst would liberate a worm with gonads occupying the entire width of the body.

According to Hopkins there is some slight possibility that *C. metoecus* and *C. cooperi* are synonymous, a point which he could not determine for lack of material. *C. metoecus,* found in bats in Europe, has never been reported in this country.

Crepidostomum isostomum Hopkins, 1931

Plate 30, Figures 2–3.

Hosts.—Type host *Aphredoderus sayanus*. In Oneida Lake, *Percina caprodes zebra* and *Percopsis omisco-maycus*. In digestive tract.

This species was originally described by Hopkins (1931) from the pirate perch of a small stream in Champaign County, Illinois, and has never been recognized from any other host or locality until found in the Oneida Lake fauna. The species is closely related to *C. farionis*, but the latter seems to be restricted to the salmonid fishes as hosts for the adult. Morphologically *C. isostomum* and *C. farionis* have many features in common but differ in a few significant points. The cirrus sac in *C. farionis* is long, often extending beyond the posterior margin of the acetabulum as a cylindrical sac within which the parts lie perfectly straight, slightly sinuous or even slightly coiled while in *C. isostomum* the cirrus sac is very short and broad, with the contained parts much convoluted.

Three specimens of Crepidostomum from *Percina caprodes zebra* and three from *Percopsis omisco-maycus* were identified as *C. isostomum*.

Body slender, sides parallel or slightly tapering. Pharynx large, 1/3 to 1/2 diameter of oral sucker, esophagus long, fork of intestine above acetabulum, genital pore anterior to fork. Ovary small, near posterior edge of acetabulum. Cirrus sac globular, containing coiled seminal vesicle. Testes rounded or irregular, close together but not contiguous, tandem, about half way between ovary and tail end of body. Vitellaria from level of genital pore to posterior tip on outside of crura, and in two rows on inside of crura from ovary to termination of crura. These last two rows are more or less discontinuous at the level of the testes, and may or may not overlap the median field behind the testes. The degree of alignment varies in different individuals.

This species appears to be uncommon in Oneida Lake.

Crepidostomum ictaluri (Surber, 1928)

Plate 30, Figures 4–11

Synonym: *Megalogonia ictaluri* Surber, 1928.

Hosts.—*Noturus flavus, Ameiurus nebulosus, A. natalis, Ictalurus punctatus,* and *Micropterus salmoides*. In the intestine.

The genus Megalogonia was created by Surber (1928:271) who on the basis of misconstrued facts stated that it is "impossible to place this distome parasite of the Channel Catfish in any family or generic group thus far recognized". A study of specimens clearly pertaining to this species, from Oneida Lake, shows that there is serious objection to considering the observed differences as of more than specific value.

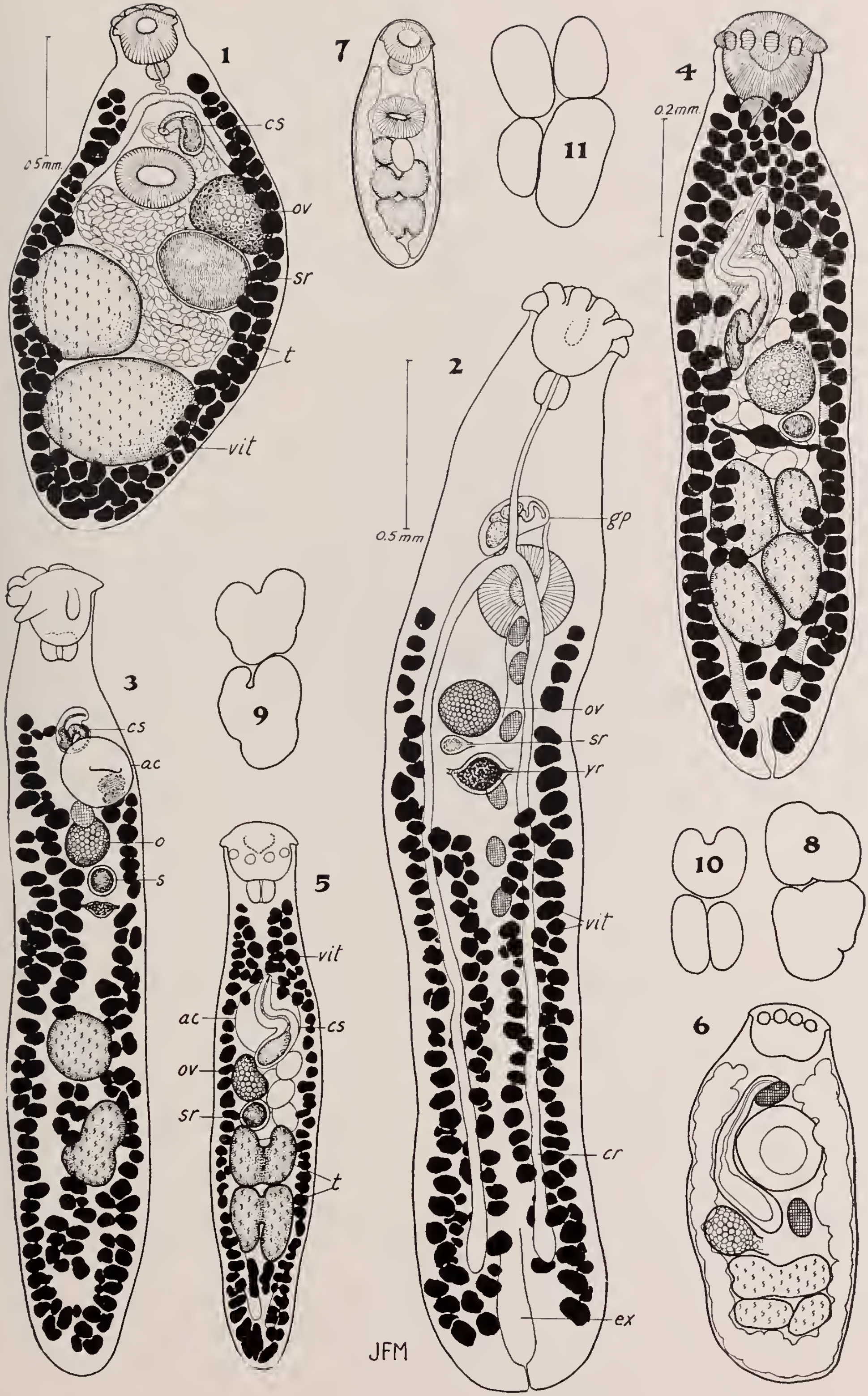
Megalogonia is differentiated from Crepidostomum on a single variable character, the condition of the testes. Typically the two testes of Megalogonia are elongated in the transverse direction and each is divided by a median constriction, forming a group of four more or less distinctly separated bodies. However, in a series of collections every stage in this transformation is observable. The testes are not invariably divided (Plate 30, Figures 8-11). We can always find in our specimens the division between anterior and posterior testes, as in Crepidostomum but frequently the right and left counterparts are demonstrably confluent. In not more than one-half of our specimens is there any clear median separation, although the transverse diameter may be relatively great. In some specimens we find partial or complete division of a single testis, the other remaining whole. Only a few show a satisfactory division to form four testes. We have examined sectioned material, and some of our whole mounts are sufficiently clear so that we have no doubts about our interpretation. L. G. Walz (1933) likewise regards the four testes as derived from two.

In all other respects the worms are typical Crepidostomum and stand very near *C. cooperi*. Moreover we have occasionally observed *C. cooperi* exhibit this

Plate 30. Papillose Allocreadiidae. (Scale with Fig. 4 applies to Figs. 4–11.) 1, *Bunodera luciopercae*, ventral view. 2, *Crepidostomum isostomum*, from Percopsis. 3, *C. isostomum*, from Percina (same scale as Fig. 2). 4, *C. ictaluri*, dorsal view of specimen from *Noturus flavus*. 5, Dorsal view of specimen from *A. nebulosus*. 6, Dorsal view of another specimen from *A. nebulosus*. 7, Ventral view of specimen from *I. punctatus*. 8–11, Testes of four individuals of *C. ictaluri* from *Noturus flavus*, showing various degrees of division.

ac—acetabulum, cr—crura, cs—cirrus sac, ex—excretory bladder, ov—ovary, sr—seminal receptacle, t—testes, vit—vitellaria, yr—vitelline reservoir.

PLATE 30


1
0.5mm.
cs
ov
sr
t
vit
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11
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0.2mm.
2
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same tendency toward division of the testes. In fact Hopkins' drawing of the type of "*C. amblopiitis*" (*C. cooperi*) shows exactly such a case of incipient division of the anterior testis. And we have found it impossible to make a decision in the identification of some of our specimens, between *C. ictaluri* and *C. cooperi*. Division of the testes is not a matter of age. Some of the smallest worms show complete division while some of the largest reveal no trace of it. We accordingly declare Megalogonia a synonym of Crepidostomum, and its single species becomes *C. ictaluri*.

Most of the specimens which we have collected range from 0.4 mm. to 1 mm. in length, but Surber has given 1.4 mm. as the length of some of his individuals. Suckers large, but comparatively thin-walled, approximately equal in size. Pharynx about ⅓ the diameter of the oral sucker. Oral papillae small. Eggs few in number, usually not more than ten; 0.064 mm. x 0.042 mm., slightly larger than those of *C. cooperi*.

Our egg-bearing specimens vary in length from 0.38 mm. to 1.0 mm. The proportion of width to length is rather greater in the small worms than in the large, the smaller possessing broad corpulent bodies, the larger having more slender outlines. While these worms present a rather heterogeneous appearance, they must, for want of any good dividing characters, all be placed under the species *C. ictaluri*.

We have about seventy-five specimens of this worm, from the hosts indicated above. The heaviest infestation was found in *Noturus flavus*, a fish of such rare occurrence in the lake that we secured only a single specimen. The *C. ictaluri* from this host are likewise the largest and most healthy looking specimens. The worms from our other hosts are smaller, and the infestations light.

All fish found to harbor this parasite were taken from near-shore locations, in shallow water, at Cleveland and vicinity, Short Point Bay, and in Chittenango Creek below Bridgeport. It would appear that the form is limited to shallow shore waters, and is of wide distribution in the lake. The channel catfish, normally a deep water resident, probably acquires its infestation on its shoreward migrations.

Crepidostomum ictaluri is preeminently a parasite of silurid fishes. We found medium infestations in the four silurids mentioned in the table. The heaviest infestation occurred in the single specimen of *Noturus flavus* from which about 75 good-sized worms were taken. The record from *Micropterus salmoides* is based on a single small specimen of the worm (0.3 mm. long), obviously immature, containing no eggs. It is not common in the bullhead, for we have only three records of its occurrence here despite the large number of this species examined by us.

Hopkins, in a manuscript thesis referred to earlier in this report, has worked on the life history of *Crepidostomum ictaluri*. He found cercariae in *Musculium transversum* and metacercariae in the gills of a mayfly (*Hexagenia limbata*), forming a parallel to the life history of *C. cooperi*. In describing the larval forms, Hopkins makes repeated comparisons with the larvae of *C. cooperi*, so it would seem that he also is impressed with the close parallelism between *C. ictaluri* and *C. cooperi*.

Genus Bunodera Railliet, 1896

The genus Bunodera has had a long and intricate nomenclatorial history. As early as 1845, Dujardin applied the subgeneric name Crossodera to those members of the old, all-inclusive genus Distoma, possessing head ornaments. Species which are now recognized as belonging to the genera Bunodera and Crepidostomum, as well as some wholly unrelated forms, were united on the sole character of head adornments. Though Dujardin's name Crossodera was pre-occupied it was continued in the literature until Railliet (1896) renamed the genus Bunodera. Though Railliet did not designate a genotype, the type of Dujardin's Crossodera, *B. nodulosa* (*B. luciopercae*), became the type of the renamed genus. The genus Crepidostomum was recognized and named by Braun in 1900. Since that date there has been conspicuous lack of agreement as to the relationships of Bunodera and Crepidostomum. Looss (1902), in founding the subfamily Bunoderinae, included both of these genera within it. Nicoll (1909) restricted the definition of the Bunoderinae and created a subfamily Stephanophialinae to include Crepidostomum and his new genus Stephanophiala. Later workers have been divided in their support of this action by Nicoll, and Odhner (1910) called attention to the fact that of the characters supposed to differentiate Crepidostomum from Stephanophiala some are based upon errors and others are not of generic value. In subsequent publications on these genera most of the authors have maintained that Bunodera and Crepidostomum are sufficiently different to warrant their separation into two distinct families. The two most comprehensive treatises on the trematodes in recent years (Poche, 1926, and Fuhrmann, 1928) assign Crepidostomum to the Allocreadiidae and recognize Bunodera as the type of the family Bunoderidae. The present writers have been unable to recognize any essential points of difference between these genera except in the form of the uterus. On the most liberal grounds such a distinction cannot be accorded diagnostic value for separation of families. The uterus is tubular in Crepidostomum and expands to form a uterine sac in Bunodera. Such a character cannot have more than generic value. Consequently we maintain that the family Bunoderidae is a synonym of Allocreadiidae, and remove the genus Bunodera to the family Allocreadiidae where it stands close to Crepidostomum. This position supports the pioneer studies of Looss (1902).

There are but few records of the occurrence of Bunodera in America. Some of the older writers have published accounts of the appearance of the European species, *B. luciopercae,* or of its synonym, *B. nodulosa,* in fresh-water fishes of this continent. These records have been under suspicion because American specimens that have been subjected to careful study have shown a number of characters at variance with the current descriptions and figures given by European investigators of high repute. S. H. Hopkins has examined specimens of *Bunodera luciopercae* obtained from European helminthologists and has informed the present writers that these worms are identical in all respects with specimens taken from American hosts. Bunodera is represented by two species in North American fishes. Both of these species, *B. sacculata,* described by Van Cleave and Mueller (1932) in Part I of this series of reports, and *B. luciopercae,* occur in the yellow perch of Oneida Lake, but the former is much more abundant.

Bunodera sacculata Van Cleave and Mueller, 1932

Hosts.—*Perca flavescens, Micropterus salmoides.* In intestine.

This form was described as a new species in the first part of this study. No new records have been secured since then. The species seems limited to the perch, and the number taken in a single fish is small, usually one or two. We have only a single specimen from *M. salmoides.* Possibly this worm is widespread in North America, but has been confused by other workers with *B. luciopercae.*

We know nothing concerning its life history. The hosts of this parasite were almost invariably taken in shallow, protected shore-line habitats. Although we examined many perch from deep water, these were almost always free from the parasite. The incidence of infestation with Bunodera is low, practically zero in the deep-water perch, and not more than 15 per cent in the shallow-water perch.

There seem to be very distinct seasonal limitations to the occurrence of this parasite in the perch. Though large numbers of this fish were examined in June and July, not a single instance of infestation appears in our records before the second week in August. During the last half of this month and early in September perch from shallow waters frequently carried a few *B. sacculata,* as did also some specimens taken in mid-winter.

Bunodera luciopercae (Mueller, 1776)

Plate 30, Figure 1

Host.—*Perca flavescens.* In intestine.

A single example of this species occurs in our collection, from Oneida Lake fishes. This specimen was taken from a six-inch perch caught through the ice in Big Bay on January 23, 1930. Nothing is known with certainty of the life history of this or any other species of Bunodera.

Genus Plagiocirrus Van Cleave and Mueller, 1932

The genus Plagiocirrus was created by the present authors (1932) to accommodate a single species, designated as *P. primus.* Both the genus and the species are described in detail in Part I of this survey. Plagiocirrus still stands as a monotypic genus with *P. primus* as its only inclusion.

Plagiocirrus primus Van Cleave and Mueller, 1932

Hosts.—*Notemigonus crysoleucas* and *Cyprinus carpio.* In intestine.

This species has been taken three times from a total of 29 golden shiners. In one shiner there were ten specimens, and in each of the other two a single worm each. Two of these fish were from Cleveland Harbor while the third came from Caughdenoy Creek.

One specimen was taken from the stomach of *Esox lucius,* which contained unidentifiable remains of several fish. The single Plagiocirrus was probably released from a golden shiner that had been taken as food. The intestine of this same specimen of Esox contained phyllodistomes which doubtless came from the urinary bladder of a perch. Esox cannot be considered as a normal host to *Plagiocirrus primus.*

Several immature, unthrifty specimens of Plagiocirrus came from the intestine of a carp taken in Short Point Bay, but in other carp examined this parasite was wholly wanting.

Nothing is known of the life cycle of this species, nor has it been recorded by any other workers since its original description.

Genus Triganodistomum Simer, 1929

Three species have been assigned to Triganodistomum: *T. translucens* (the type), *T. attenuatum* and *T. simeri.* The last two were founded on specimens taken from the common sucker (*Catostomus commersonnii*) of Oneida Lake, and named by the present authors in Part II of this report.

Key to the Species of the Genus Triganodistomum

(An asterisk (*) denotes species found in Oneida Lake.)

1 (a) Body length about 3.5 mm. Testes in middle third of body............**T. attenuatum***
(b) Body length 1.5 mm. or under. Testes in posterior half of body................. 2
2 (a) Vitellaria almost wholly lacking in posterior third of body. Uterus extends behind posterior testis for a distance equivalent to the length of the zone of the gonads ....**T. simeri***
(b) Vitellaria extend from acetabulum to near posterior tip of body. Uterus only slightly posterior to testes..**T. translucens**

Triganodistomum attenuatum Mueller and Van Cleave, 1932*

Host.—*Catostomus commersonnii.* In intestine.

A total of six specimens of this species have been included in our collections and these came from two individuals of the common sucker, one a fingerling from Cleveland Harbor, June 24, 1931, and the other from the mill pond in Cleveland, July 9, 1931. Thirty-four other suckers examined from the same vicinity revealed no additional specimens of this parasite. The worm appears to be more abundant in younger suckers. Nothing is known of its life history.

Triganodistomum simeri Mueller and Van Cleave, 1932*

Host.—*Catostomus commersonnii.* In intestine.

Two individuals of the common sucker provided the eleven worms of this species in our collections. One of these was the same small sucker recorded (June 24, 1931) as host for *T. attenuatum.* The other was a large sucker from Black Creek (July 9, 1931). Ten individuals were found in the small and one in the large sucker. Since the original description both this and the preceding species have been taken in suckers from a number of additional localities around the shores and in the tributaries of Oneida Lake. Both species are apparently more abundant in the young suckers.

* For a detailed study of this species see Part IV.

Genus Macroderoides Pearse, 1924

Synonym: *Plesiocreadium* Winfield

The genus Macroderoides was erected by Pearse (1924:148) to contain as type a trematode which he designated as *M. spiniferus,* from the short-nosed gar and from two species of bullhead from Lake Pepin, Wisconsin. Winfield (1929), apparently unaware of Pearse's work, created a new genus, Plesiocreadium, for his own new species *P. typicum,* taken in Amia from Douglas Lake, Michigan. The present writers (Van Cleave and Mueller, 1932) have considered Plesiocreadium Winfield as a direct synonym of Macroderoides Pearse. Subsequent studies have added further confirmation to the validity of this position, even though Hunter (1932) independently compared the two genera and dismissed the resemblances as superficial. Without giving any of his evidence, Hunter states that "A careful study of section material dispels this delusion". Though he found it necessary to modify Winfield's characterization of the genus Plesiocreadium before it would accommodate his new form, no information given in his emended characterization nor in his figures or description of *P. parvum* stands in conflict with the concept of the genus Macroderoides held by the present writers, or set forth in a redescription of the genus based upon a re-examination of the type by Simer (1929). Consequently the present writers reaffirm their conviction that Plesiocreadium is a direct synonym of Macroderoides. Four species are therefore included in this genus.

Key to the Species of the Genus Macroderoides

(An asterisk (*) denotes species found in Oneida Lake fish.)

1 (a) Length of body at least six times maximum width. Forebody distinctly flattened dorso-ventrally 2
(b) Body spindle-shaped, length not more than five times maximum width. Forebody not flattened 3
2 (a) Vitellaria not extending posterior to the second testis .... **M. spiniferus**
(b) Vitellaria continuing beyond second testis into posterior tip of body .... **M. parvus**
3 (a) Prepharynx wanting. Body widest between suckers .... **M. typicus**
(b) Prepharynx present. Body widest posterior to acetabulum .... **M. flavus***

With regard to host relations, *M. typicus* has been reported from *Amia calva* only; *M. flavus* from *Esox niger* only; *M. spiniferus* from two species of Lepisosteus and two of Ameiurus; and *M. parvus* from *Lepisosteus osseus* and *Amia calva.*

Macroderoides flavus Van Cleave and Mueller, 1932

Host.—*Esox niger.* In intestine and rectum.

We have records of eight infestations with this parasite, from *Esox niger,* for which it seems very specific. The infestation is usually very light, 10 to 20 worms in a fish. However, one fish taken in Big Bay, July 5, 1929, had about fifty, while two taken from the same locality on December 26, 1930, had together about 500 of these worms in the intestine.

Out of fifty pickerel from comparable habitats, eight were infested and forty-two non-infested with *M. flavus.* Five of the fifty pickerel were taken during the winter, and forty-five during the summer. All five of the winter fish were infested, but only three of the forty-five summer fish. It therefore appears that *M. flavus* reaches its maximum abundance in the winter and drops off during the summer. This is exactly the opposite from *M. spiniferus* which was found by Simer to be most abundant during the summer.

The specificity of this parasite for its host *E. niger* is remarkable, for in seventeen carefully examined specimens of the closely related *Esox lucius* not a single worm was found, although these fish were often taken from the same habitat whence infested pickerel had been secured.

The life history of this species is unknown.

Genus Alloglossidium Simer, 1929

Synonym: *Plagiorchis*, in part.

In 1921 Lamont described a new species of trematode from *Schilbeodes gyrinus*, under the name *Plagiorchis corti*. This was the first assignment of a fish trematode to this characteristically avian and mammalian genus of parasites. As pointed out in the present report under the discussion of the family Allocreadiidae, the fish trematodes which have been assigned to Plagiorchis do not have a Y-shaped excretory bladder and hence should be excluded from the family Plagiorchiidae as currently characterized. In recommending this action the present writers take the position that Simer's generic name Alloglossidium is available for *P. corti* and *P. geminus*. The species which Simer (1929) described as *A. kenti* is very clearly a renamed *P. corti*. Hence the valid species *Plagiorchis corti*, by transfer to Alloglossidium, becomes *A. corti* and takes the place of its synonym *A. kenti* as type of the genus Alloglossidium.

In addition to the above synonymy, it should be noted that Mueller (1930) has detailed the evidence for considering *P. ameiurensis* McCoy, 1928, as a synonym of *Alloglossidium corti*. Thus of four specific names introduced into the literature two are reduced to synonymy, leaving but two valid species distinguishable on the basis of characters used in the following key.

Key to the Species of the Genus Alloglossidium

(An asterisk indicates species known to occur in the Oneida Lake fish.)

1 (a) Anterior follicles of vitellaria at or anterior to the midpoint between pharynx and acetabulum .... **Alloglossidium corti***

(b) Anterior follicles of vitellaria never anterior to acetabulum. **Alloglossidium geminus***

We have Alloglossidium from the following hosts: *Schilbeodes gyrinus, S. miurus, Ameiurus nebulosus, A. natalis, Ictalurus punctatus,* and *Ambloplites rupestris*. More than five hundred specimens of Alloglossidium are in our fish parasite collection. An intensive study of this material has left us somewhat in doubt as to the actual number of species represented. Since most of the variable characters are intergrading, we recognize but two species as set forth in the foregoing key.

Alloglossidium corti (Lamont, 1921)

Text Figure 3, Figures 2–3

Synonyms: *Plagiorchis corti* Lamont, 1921; *Plagiorchis ameiurensis* McCoy, 1928; *Alloglossidium kenti* Simer, 1929

Hosts.—*Schilbeodes gyrinus, S. miurus, Ictalurus punctatus, Ameiurus natalis, A. nebulosus, Ambloplites rupestris.* In intestine.

The specimens found in *S. gyrinus* are typical *A. corti*, from which specimens in other hosts show varying degrees of individual difference. Length 1 mm. to 2 mm., thickness almost equal to the width. Worms colorless and transparent in life. When placed in tap water the eggs are shed at once. Individual eggs yellowish but in mass appear darker, imparting to the uterus a brown color; 0.028 mm. by 0.016 mm.

The vitellaria are the chief diagnostic character separating this species from the following. The posterior follicles are usually at the level of the anterior edge of the second testis. The anterior follicles lie at, or anterior to, mid-level between the pharynx and acetabulum. Occasionally they are on a level with the pharynx.

We have four specimens of *Alloglossidium corti* from *Schilbeodes miurus* taken in the trawl in about 20 feet of water off Jewell, N. Y. These worms are about 1.55 mm. long. In general topography they are very similar to specimens taken from the catfish, but the gonads are much smaller, the uterus more crowded with eggs, and the ovary is slightly lobate.

Our few specimens of Alloglossidium from *Ameiurus natalis* show distinctly the two types of anatomy definitive for *A. corti* and *A. geminus*. Both occur together in the same host individuals. McCoy (1928) found a form in *Ameiurus natalis* in Ramona Lake, near St. Louis, Mo., to which he gave the name *P. ameiurensis*. Further study of this form and comparison with the type specimen of *A. corti* by Mueller (1930) proved these two species to be synonyms.

We have one much distorted specimen of *A. corti* from *Ambloplites rupestris*. The crura are unusually short. The uterus is very voluminous and densely crowded with eggs. The vitellaria are, however, diagnostic of *A. corti*.

Alloglossidium geminus (Mueller, 1930)

Text Figure 3, Figure 1

Synonym: *Plagiorchis geminus* Mueller, 1930

Hosts.—*Ameiurus natalis, A. nebulosus.* In intestine.

Length 1 mm. to 1.5 mm. In life of a distinctly pinkish color. Eggs of varying size, from 0.024 mm. x 0.012 mm. to 0.032 mm. x 0.016 mm. Ovary rounded, in contrast to *A. corti*, in which it is frequently irregular or lobate. Anterior vitelline follicles approximately on level with anterior edge of acetabulum, or farther back, never anterior to acetabulum.

Biology of Alloglossidium.—In this lake six species of fish have been found carrying Alloglossidium. One of these records (the rock bass) is based upon the presence of a single aberrant worm. The five remaining hosts are all members of the Siluridae. *A. corti* occurs in all five of these fishes, whereas, *A. geminus* is found only in *Ameiurus nebulosus* and *A. natalis,* occasionally in multiple infestations with *A. corti.*

Infestation of *Schilbeodes gyrinus* with *A. corti* in the Bridgeport tributary of Chittenango Creek is very high—only 1 out of 8 being uninfested, the number of worms per fish ranging from 10 to 50. In the three catfish examined about 10 to 15 *A. corti* were found per fish. About 30 per cent of the common bullheads carry *A. geminus,* the number per fish being usually around five or six. The only hosts harboring both species are *Ameiurus natalis* and *A. nebulosus.* *A. natalis* is uncommon, and an unimportant host of the genus. *Ameiurus nebulosus* is the chief host of *A. geminus,* and we have found the fish infested with this species in shoreline situations and inflowing streams—such as Caughdenoy, Chittenango and Fish creeks. Only two instances were found of this fish harboring *A. corti.* One of these was from the small tributary of Chittenango Creek at Bridgeport. This fish harbored only *A. corti.* The other fish was from Caughdenoy Creek, and carried both *A. corti* and *A. geminus* in small numbers.

Fig. 3. Alloglossidium. 1, *Allogtossidium geminus,* from *A. nebutosus,* dorsal view. 2, *A. corti,* from *S. gyrinus,* ventral view. 3, *A. corti,* from *I. punctatus,* dorsal view.

ex—excretory bladder, gp—genital pore.

In the deep water *A. corti* is found in *Ictalurus punctatus* and *Schilbeodes miurus,* and in tributary streams in *Schilbeodes gyrinus,* but seems scarce in the littoral zone, whereas *A. geminus* occurs in the littoral zone, in *A. nebulosus* and *A. natalis.* Whether host limitations or habitat are responsible for this differential distribution is not clear.

McCoy, 1928, found small crayfish in Ramona Lake, Mo., infested with cysts of a xiphidiocercaria. Upon feeding these to young *Ameiurus natalis,* he secured an infestation of *"Plagiorchis ameiurensis"*=(*A. corti*). Thus *A. corti* is transmitted by crayfish. The cercariae of this same worm were found in *Planorbis trivolvis.* Presumably the life history of *A. geminus* is very similar.

Family Heterophyidae

In Part II of this survey, the present writers have given detailed attention to the Heterophyidae of fresh-water fishes of North America. Seven genera, all represented in the Oneida Lake fauna, were shown to conform to the heterophyid concept as follows: Vietosoma, Acetodextra, Cryptogonimus, Caecincola, Centrovarium, Neochasmus, and Allacanthochasmus. An eighth genus, Apophallus, reaches maturity in water birds, but has been recorded also from fishes of Oneida Lake. Since the time of publication of Part II, Mueller (1933; and part IV published with this paper) has made a detailed restudy of these genera, and shown that Vietosoma possesses a cirrus sac, and must hence be excluded from the Heterophyidae.

Genus Acetodextra Pearse, 1924

Pearse (1924) proposed the name Acetodextra for a genus of peculiar trematodes from the air bladder of catfishes. These worms Stafford (1900) had described almost a quarter of a century earlier, but they remained practically unstudied and unrecorded by later writers until Pearse directed attention to them. Even after the group had been named, no one ventured to locate it in the general system of the trematodes until the present writers (1931) assigned it to the Heterophyidae and later (1932) presented further evidence in support of this assignment.

The air bladder of fishes is such a specialized habitat that very few species of trematodes have ever become established in this organ. In 1927 Odhner published a review of the trematodes dwelling in the air bladder, but at that time he was evidently not acquainted with Pearse's paper in which the genus Acetodextra was defined. Southwell (1913) described Isoparorchis from a silurid of the East Indies, and Kobayashi (1921) described what he considered to be a new genus from a Japanese silurid, and to which he applied the name Leptolecithum. Later workers have reviewed the evidence and have declared that Leptolecithum is identical with Isoparorchis. This claim of synonymy has been advanced by Travassos (1923) and maintained by Bhalerao (1926), by Poche (1926) and by Odhner (1927). Though the genitalia of Isoparorchis in some measure resemble those of the Heterophyidae, the genital atrium bears no direct connection with the ventral sucker. Most recent authorities place Isoparorchis in a separate family of which this genus is the type.

It is interesting to note that in different parts of the earth two different genera representing different families of trematodes have taken up their abode in the air bladders of fishes. Further, it seems significant that these forms should be restricted to the catfishes. This is probably related to the fact that the duct of the air bladder remains open throughout life in these fishes.

We have taken this worm from only two hosts — the common bullhead (*Ameiurus nebulosus*) and the yellow bullhead (*A. natalis*). In all, about seventy-five of the first and four of the second were examined for Acetodextra. The rarity of *A. natalis* in Oneida Lake accounts for the small number of examinations of this species. About ninety-five specimens of Acetodextra are included in our collections, of which only five are from the yellow bullhead. Our specimens belong to the single species, *Acetodextra amiuri,* the type of the genus. As no other member of this genus has been found since the time of its founding in 1924, the genus still rests on the genotype.

Acetodextra amiuri (Stafford, 1900) Pearse, 1924*

Text Figure 5, Figure 1

Hosts.—*Ameiurus nebulosus* and *A. natalis.* In air bladder.

These are fair-sized trematode worms found in the air bladder of bullheads. They are creamy or colorless in life except for the dark brown eggs filling the uterus and showing through the body wall. Suckers are weak and the worms show almost no motion. These worms range in size from 0.75 mm. to 3 mm. in length. They are of varying shape and outline. Usually they have the form of a small seed, the oral sucker being at the pointed end. Posteriorly, the outline tends to be truncated and irregular, at times with a slight median notch. The proportion of length to breadth of the body ranges from elongate to almost circular outline. The dorsal surface of the body is strongly arched, especially in older specimens in which the internal pressure of the uterine eggs is relieved chiefly by the bulging of the surface. The ventral side is flat, and in the region of the acetabulum and gonotyl is noticeably depressed. From the floor of the cavity of the gonotyl there arises a tongue-like structure which fills most of the available space and has its tip protruding into the groove leading to the exterior.

We have frequently found large specimens in the air bladder, greatly distended with eggs, which in view of their weak and devitalized appearance gave evidence of degeneration of their tissues. Such specimens were apt to burst upon handling or upon introduction into the fixing fluid. When worms were found in the air bladder, we usually found no masses of eggs; however, on several occasions large clumps of eggs were taken from air bladders in which no worms were found. It seems safe to infer that Acetodextra retains its eggs while alive. The worms apparently die and disintegrate *in situ,* whereupon the uterine eggs are released to become lodged in clumps in the recesses of the air bladder. Since the eggs have no provision for penetrating the tissues of the host, they doubtless escape to the exterior upon its death and disintegration.

Of fifty-six common bullheads examined specifically for Acetodextra, only eight harbored these worms. Most of these eight bullheads were taken in Cleveland Harbor, though we also have records of Acetodextra in the same species from the sloughs of Fish Creek and Fairchild Bay. Bullheads which we examined from the mill pond at Cleveland and from Short Point Bay carried no infestation with this parasite. The degree of infestation likewise fluctuates within wide limits. Only one or two worms were present, as a rule, but in two exceptional cases we found thirty and fifty, respectively.

All of the four yellow bullheads which we examined came from the immediate vicinity of Cleveland. The two infested with Acetodextra bore in one instance a single worm and in the other four.

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* For a detailed study of this form see Part IV.

It seems that in the region studied the percentage of infestation in the common bullhead is approximately 15 per cent. Our records are inadequate to allow correlation with season or habitat.

On two occasions we have taken very minute Acetodextra from the alimentary canal of the common bullhead. These fish were taken July 20, 1929, and July 25, 1931, respectively, the former from Fairchild Bay and the latter from Cleveland Harbor. In each instance the worms were less than one millimeter in length, and immature in the sense that they did not bear eggs, though all the internal organs were well formed. Since the air bladder in the silurids (Physostomi), communicates with the digestive tract, it seems probable that these small worms from the gut were on their way to the air bladder.

Beyond this conjecture nothing further is known concerning the life cycle of Acetodextra.

Genus Cryptogonimus Osborn, 1903

The members of the genus Cryptogonimus are small, delicate worms about 1 mm. long, found in the digestive tract of certain predacious fishes of North America. The body is colorless and almost transparent except for the dark brown or blackish eggs in the uterus, which are visible through the thin body wall.

The genus seems to be limited to this continent where its form and fundamental structure are closely paralleled by the genera Caecincola and Allacanthochasmus (as represented by *A. artus*). As pointed out in an earlier paper (Mueller and Van Cleave, 1932) these genera from North American fishes constitute a distinctive group of heterophyids not paralleled in the faunas of other parts of the earth.

A single species, *C. chyli*, has been recognized in this genus. The scanty records of its occurrence in the literature indicate that it is probably limited to the northern states and Canada. All of our specimens from Oneida Lake conform to the type of the genus.

Cryptogonimus chyli Osborn, 1903*

Text Figure 4, Figure 1

Hosts.—*Ambloplites rupestris* and *Micropterus dolomieu*. In digestive tract.

Specific Description.—Length of a typical individual 0.88 mm. Middle third of body of about uniform width (0.180 mm.), tapering at each extremity. Oral sucker prominent, funnel-shaped, opening straight forward. Prepharynx, pharynx, and esophagus well developed. Crura enter the posterior third of body, terminating in the region of the testes. Excretory bladder Y-shaped, the two arms extending forward to the level of the pharynx where their greatly expanded tips occupy practically the entire width of the body. Eye spots present. Vitellaria lateral, follicular, in middle third of body arching somewhat over dorsal surface. Ventrogenital complex slightly posterior to fork of intestine. Acetabulum small (about 0.05 mm. in diameter) and submerged in the genital atrium. Anterior to it a cylindrical gonotyl. The common genital duct opens into the atrium between acetabulum and gonotyl and receives two branches, the dorsal seminal vesicle and the ventral metraterm. The uterus forms a single sling passing posteriorly from the

* For a detailed study of this form see Part IV.

ovary to near the posterior tip of the body, looping and proceeding forward to pass to the genital sinus. In large individuals the uterine coils fill the posterior third of the body. Uterine eggs almost black. Testes oblique, near tips of crura. Ovary lobate immediately anterior to testes. Seminal receptacle present.

Only two species of fish have been found as normal hosts of *C. chyli*—the rock bass and the small-mouth black bass. We once found a single immature specimen in a bullhead, but this is obviously an accidental occurrence. This evidence of sharp host limitation is supported by the records of Cooper (1915) and of Pearse (1924a).

Neither of the normal hosts is heavily infested with this worm during the summer months. We consider fifty worms to represent heavy infestation by this species in Oneida Lake, but the number in most instances was considerably less.

The relative infrequence of Cryptogonimus in Oneida Lake stands in sharp contrast to its reported abundance elsewhere. Bangham (1926:118) reports that "The adults of this species were found in the pyloric caeca and upper intestine of nearly all the small-mouth bass, large-mouth bass, and rock bass examined. This trematode occurred as an adult first when the bass reached a size of 45 to 50 mm. They were not found sexually mature in younger bass."

In our studies, incidence of infestation seems rather clearly correlated with the habitat of the fish. Infestation is more frequent in open water, over gravel bottom, than in protected shore situations. Both species of normal hosts are to some extent migratory, hence recorded place of capture cannot be taken as the permanent dwelling place of the specimen. Of four infested small-mouth black bass, three were taken on the gravel bar in open water off Jenning's Point, Cleveland. The fourth was from 50 feet of water off Cleveland. In six *M. dolomieu,* negative for Cryptogonimus, three were fingerlings, probably not yet feeding on the larval host of this parasite, and three were large fish from habitats similar to or identical with those producing infested bass.

Of the infested rock bass, four were taken on the gravel bar off Jenning's Point and one in Cleveland Harbor at the mouth of Black Creek, but obviously from the lake since it was caught in the lake side of a gill net stretched across the creek. Another infested rock bass was from Fairchild Bay. This is the only instance of infestation in a fish from shallow water. Seven rock bass from relatively protected shore-line localities were all negative for Cryptogonimus.

The adult *M. dolomieu* is normally a fish of deep, open water. Roughly our records indicate about 50 per cent incidence of infestation for this species. The rock bass, however, is less of an open water fish and more given to inhabiting shore-line situations. In this species individuals living inshore are practically free from Cryptogonimus while offshore the infestation approaches 100 per cent. We regard the open water rock bass as the natural host of Cryptogonimus, with *M. dolomieu* occupying an important secondary position.

Genus Caecincola Marshall and Gilbert, 1905

Because of the close agreement in structure of Caecincola and Cryptogonimus, the present writers (1932) ascribed the genus Caecincola to the family Heterophyidae. A single closely knit species, wholly restricted to North America, is the sole representative of the genus.

Caecincola parvulus Marshall and Gilbert, 1905*

Text Figure 4, Figure 2

Host.—*Micropterus salmoides.* In stomach, ceca and intestine.

Originally described from the large-mouth black bass, the species *C. parvulus* is wholly restricted to this host in Oneida Lake, though Pearse (1924) has recorded *M. dolomieu* and *Ambloplites rupestris* as hosts in Wisconsin lakes. Not a single specimen of either of the two last named fishes has been found infested with Caecincola in Oneida Lake.

Small delicate, vase-shaped worms about 0.5 mm. in length, which, during life, move but feebly and disintegrate quickly after removal from the host. Oral sucker flaring or cup-shaped. Behind oral sucker the body may be constricted to form a neck. Maximum diameter in region of acetabulum. Posterior extremity pointed. Prepharynx and esophagus short. Pharynx well developed. Crura fork at level of acetabulum, widely divergent and very short, terminating near middle

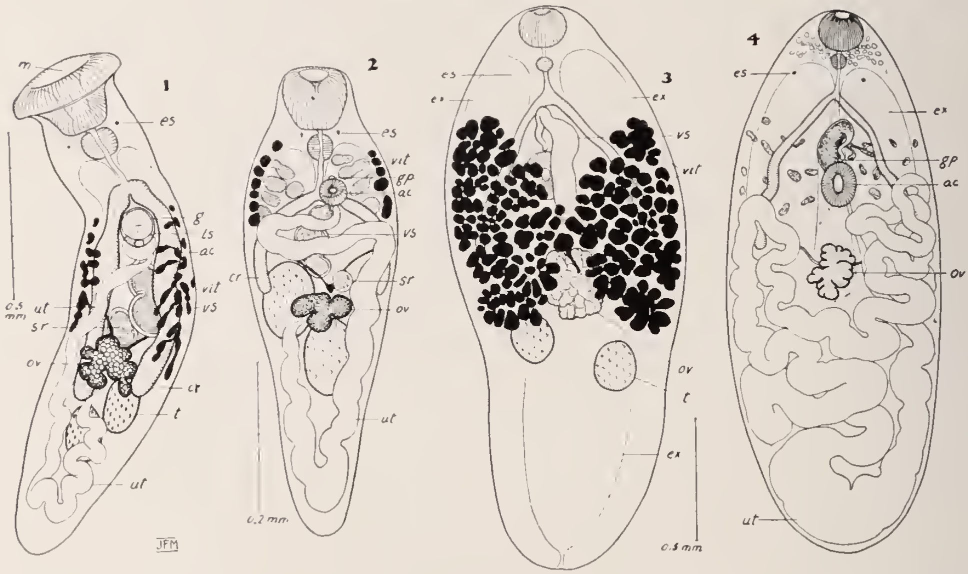

Fig. 4. Heterophyidae. 1, *Cryptogonimus chyli*, ventral view, specimen with widely expanded oral sucker. 2, *Caecincola parvulus*, ventral view. 3, *Centrovarium lobotes*, dorsal view of metacercaria from Percopsis. 4, *C. lobotes*, ventral view of adult worm, same scale as 3.

ac—acetabulum, cr—crura, es—eyespots, ex—excretory bladder, g—gonotyl, gp—genital pore, ls—lip of ventro-genital sinus, m—mouth, ov—ovary, sr—seminal receptacle, t—testes, ut—uterus, vit—vitellaria, vs—seminal vesicle.

of the body or anterior to it. Ovoidal testes near ends of crura, lateral or oblique. Ovary with three small, rounded lobes; anterior to testes, near center of body. Acetabulum much smaller than oral sucker, the genital pore at its anterior margin. Vitellaria restricted to anterior third of body, lateral clusters of distinct follicles arching somewhat over the dorsal surface. Right and left vitelline ducts pass

* For a detailed study of this form see Part IV.

obliquely backward toward the ovary. Uterus makes a single loop in the posterior region of the body. Seminal vesicle present, constricted into several parts, continuous with dorsal branch of the common genital duct. No cirrus or copulatory apparatus. Seminal receptacle present. Excretory bladder Y-shaped, its two branches extending forward to the region of the pharynx. Eye spots present. Eggs pale yellow when first formed, but as they pass down the uterus the shell becomes dark brown and finally almost black. Upon opening the gut of a black bass carrying a heavy infestation of Caecincola, it appears as though a multitude of black specks had been sprinkled through the whitish chyle and mucus.

Micropterus salmoides is the only host in which we have found Caecincola in Oneida Lake. The large-mouth bass is an inhabitant of weedy shore waters, with muddy bottom. All of our records of Caecincola were secured from bass taken in such a habitat, and are for the month of August, most of them being restricted to the latter part of the month. None of the bass examined in June and July carried this parasite, but approximately 50 per cent of the large-mouth bass examined in August yielded Caecincola. Individual infestations vary greatly. From 10 to 50 worms were usual numbers found in a single fish, but one black bass thirteen and one-half inches in length taken on the north shore of Short Point Bay on August 29, 1929, carried a mass infestation of several thousand.

Caecincola and Cryptogonimus evidently occupy parallel niches in the ecology of the lake. Occurring in the same lake these two genera are selective for different hosts and do not overlap in their habitats. Cryptogonimus occurs in about 50 per cent of the deep water small-mouth bass and rock bass while Caecincola has the same relative frequence in the shallow-water large-mouth bass. Agreement in general appearance of the two worms and their location within the host are evidence of parallelism induced by similar relations to the environment.

Genus Centrovarium Stafford, 1904

The genus Centrovarium is apparently restricted to North American freshwater fishes. Stafford in 1904 created this genus which he based on *Distomum lobotes* of MacCallum as type. There have been but scanty references to the genus in the literature and many authors have been wholly non-committal as to its relationship. In Part II of this survey, the present writers (1932) have restudied the relations of this genus and on the basis of detailed morphological agreement between its members and Caecincola and Cryptogonimus, assigned Centrovarium to the family Heterophyidae and subfamily Heterophyinae. Poche (1926) failed to make any satisfactory assignment of this genus as reflected in the fact that he included it in a list of genera having uncertain relations, but appended it to his super-superfamily Fasciolida.

The worms are of moderate size and of delicate structure. In life they show little or no activity when removed from the gut of the host. The living worms are whitish or light brown in color. Both metacercariae and adults have been found in Oneida Lake fishes. All of our specimens belong to a single species, the type of the genus.

Centrovarium lobotes (MacCallum, 1895)*

Text Figure 4, Figures 3–4

Hosts.—*Perca flavescens, Stizostedion vitreum, Micropterus dolomieu, Ameiurus natalis.* In intestine. Metacercariae encysted in *Percopsis omisco-maycus.*

Ellipsoidal worms about 2 mm. in length, with very fragile structure. Musculature very weakly developed. Voluminous Y-shaped excretory bladder extends forward to level of pharynx. Ovary rosette-shaped near center of body. Intestinal crura not reaching the ovary. Seminal vesicle passes far forward of the acetabulum. Numerous brown or straw-colored eggs about 0.032 mm. x 0.015 mm.

We have found the trout perch (*Percopsis omisco-maycus*) rather generally infested with metacercariae of Centrovarium. These metacercariae are fully as large as the adults and in some respects are much more favorable for study. They are milky white in color and the vitellaria stand out in great brilliancy. In the adults the ovary, testes and vitellaria are so degenerate that it is frequently impossible to detect them at all, while the encysted metacercariae show these organs at the height of their development and in perfect detail. Cysts of the larvae in the trout perch were especially abundant beneath the skin in the region of the branchiostegals, but specimens were generally distributed throughout the body. Each was surrounded by a clear cyst wall. Some of the larger metacercariae already contained a few eggs in the uterus.

Hunter (1930) found metacercariae in the body cavity, flesh, between the myotomes and in the eye sockets of minnows from Sucker Brook, near Waddington, N. Y. *Micropterus dolomieu* fed experimentally with infested minnows at the end of six days yielded sexually mature *C. lobotes.*

Percopsis is the only fish in Oneida Lake in which we have found metacercariae of Centrovarium, but our studies on minnows have been very limited. According to our records, Centrovarium is the most abundant and general parasite of Percopsis in the area studied. The number of metacercariae which we have found is disproportionately large considering the scarcity of adult worms.

Percopsis is very abundant in Oneida Lake. In beam trawl collections it has been the most abundant fish taken, as many as 200 having been secured in a single haul from deep water. It apparently prefers deep waters most of the time, where it travels in large schools close to the bottom.

We have but eleven egg-bearing individuals of Centrovarium and these were taken from four different species of hosts. All but one of these were captured with gill nets set in deep water in the vicinity of Cleveland. The exception was a yellow bullhead caught in a gill net at the mouth of Black Creek. That this last named was proceeding from the lake into the creek is indicated by the fact that it entered the net on the lake side. One yellow perch from deep water contained seven worms; one pike perch, two worms; one small-mouth black bass, three worms; and one yellow bullhead, three worms. In Oneida Lake, the deep waters furnish conditions most favorable for infestation by *Centrovarium lobotes,* due to the abundance of Percopsis, which carries the metacercariae, in this habitat.

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* For a detailed study of this form see Part IV.

Genus Neochasmus Van Cleave and Mueller, 1932

The genus Neochasmus was described by the present writers in Part I of this report (1932), and a new subfamily, the Neochasminae, was created within the Heterophyidae to accommodate this peculiar genus. Still further details of morphology and relationships were set forth in Part II of this survey (1932) to which the reader is referred for a diagnosis of the genus. The type species on which the genus was founded remains the sole species recognized to date.

Neochasmus umbellus Van Cleave and Mueller, 1932

Hosts.—*Micropterus salmoides, Boleosoma nigrum olmstedi* and *Necturus maculosus.* In the intestine.

Small trematodes with a circumoral ring of spines. Body colorless except for the brown eggs visible through the body wall. Even in unstained specimens this species is readily distinguishable from its near relatives of the genus Allacanthochasmus by the appearance and location of the acetabulum which in Neochasmus is at the level of the intestinal fork.

Seven specimens from the large-mouth black bass were designated as cotypes of *N. umbellus.* The bass which served these as host was taken on the west shore of Walnut Point, August 27, 1929. Two worms from a *Boleosoma nigrum olmstedi* captured by the beam trawl in deep water off Cleveland on August 21, 1931, were in our collections when the cotypes were designated, but by oversight were not mentioned. Similarly a mud puppy (*Necturus maculosus*), taken by ice fishing on February 28, 1931, yielded one specimen of Neochasmus. We have thus encountered a total of nine individuals of Neochasmus, all of which are sexually mature. A careful search through our collections and special attempts at locating additional sources of material have proven unfruitful and have forced the conclusion that the species is uncommon in Oneida Lake.

We have not found any immature specimens and know nothing of the development in intermediate hosts. Our scanty records may perhaps be attributed to the fact that we have not encountered the normal host, or to seasonal periodicity of infestation.

Genus Allacanthochasmus Van Cleave, 1922

The genus Allacanthochasmus is phylogenetically related to Neochasmus. The authors have emphasized this point in Parts I and II of this report, and in the latter placed the genus Allacanthochasmus and Neochasmus together in the same subfamily of the Heterophyidae.

In the ten years since the genus was first recognized there have been few references to it in the literature and these were almost exclusively attempts to assign the genus to a place in the general trematode system. All evidence seems to indicate that this genus in common with other heterophyids of fresh-water fishes is peculiarly American.

Allacanthochasmus varius Van Cleave, 1922*

Text Figure 5, Figure 2

Hosts.—*Lepibema chrysops.* In intestine. Metacercariae encysted in various fishes, especially minnows.

1.0 mm. to 1.3 mm. in length by 0.28 mm. to 0.30 mm. in width. Body robust, dorso-ventral diameter somewhat less than width. Oral sucker terminal, well rounded, bearing on its anterior face a crown of heavy spines 26 to 29 in number. Prepharynx and esophagus very short or lacking. Pharynx one-half the size of the oral sucker. Crura pass to near the posterior tip. Gonotyl anterior to acetabulum, never withdrawn into sinus. Cuticula immediately surrounding it greatly thickened, and immediately anterior to the gonotyl, devoid of spines. Common genital duct between the gonotyl and the acetabulum. Acetabulum, though well developed, is not quite two-thirds the size of the oral sucker. Ovary a transverse lobate band of follicles, behind acetabulum. Testes spherical, lateral or slightly oblique, posterior to ovary. Vitellaria from ovary to near fork of crura, in the anterior region continuous over the back. Uterus in posterior third of the body with ascending and descending stem, thrown into transverse loops which extend out to the edges of the body. Eggs thin-shelled, dark brown, 0.020 mm. x 0.012 mm. Seminal vesicle anterior to acetabulum. Seminal receptacle anterior to ovary and dorsal to acetabulum. Eye spots present. Body with delicate spination over its entire surface.

The biological relationships of this and the following species are discussed later.

Allacanthochasmus artus Mueller and Van Cleave, 1932*

Host.—*Lepibema chrysops.* In intestine.

This form was described by us in Part II. In general, the species presents a striking similarity to Cryptogonimus. It differs from *A. varius* in that the ovary has fewer lobes. The uterus is smaller, consisting of a single sling in the posterior third of the body, with a descending and ascending stem loosely winding, and the eggs appear somewhat lighter in color. The testes are sharply oblique or subserial. Vitelline follicles scarcer but similar in distribution to those of *A. varius.* Seminal receptacle present. Gonotyl a stalk-like cylindrical organ on anterior lip of ventro-genital sinus. At its apex it bears five blunt processes. The adjacent cuticula is thicker than that over the general body surface. The seminal vesicle in this species lies largely posterior to the acetabulum, contrary to the condition found in *A. varius.* The oral sucker is funnel-shaped, and bears 26 to 29 cuticular spines. A pair of vestigial eye spots is present.

Biological Relationships of Allacanthochasmus.—We have in our collections about 2,000 specimens of Allacanthochasmus. The proportion of *A. varius* to *A. artus* is about 25:1. Both of these species we found regularly and coincidently infesting *Lepibema chrysops,* in the above proportion. The adult white bass, although plentiful in certain regions of the lake, is difficult to secure except

* For a detailed study of this form see Part IV.

by trapping at certain seasons. We examined six adults, all from Billington Bay. While these fish were infested with a variety of worms, in each case Allacanthochasmus was the most abundant. Each of the fish harbored from 300 to 500 worms, representing a mixed infestation of both *A. varius* and *A. artus.*

We have also examined fifteen fingerling white bass, taken in the beam trawl in about forty feet of water off Cleveland. These young were about three inches long. While they bore a relatively large parasite burden, few Allacanthochasmus were included.

We have found the cysts of Allacanthochasmus abundant in minnows, which when eaten by the white bass are doubtless the medium of transfer of the worms to the final host. In one case sixty of these cysts were taken from a minnow found in the stomach of a small white bass. Of the fifteen fingerling white bass examined, ten were completely free of Allacanthochasmus, four harbored only two or three of the worms, while the fifth one contained the heavily infested minnow just mentioned besides a number of small recently excysted worms.

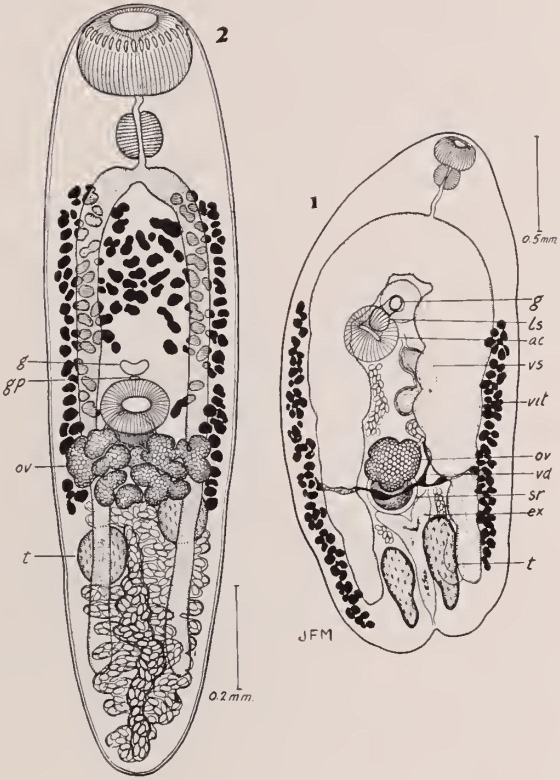


Fig. 5. Heterophyidae. 1, *Acetodextra amiuri,* ventral view. 2, *Allacanthochasmus varius,* ventral view.

ac—acetabulum, ex—excretory bladder, g—gonotyl, gp—genital pore, ls—lip of genital sinus, ov—ovary, sr—seminal receptacle, t—testes, vd—vitelline duct, vit—vitellaria, vs—seminal vesicle.

The reason for this marked contrast between old and young white bass in Allacanthochasmus infestation is to be found in the food habits of the fish. The young fish subsist on a diet of Entomostraca, and are heavily infested with adolescentia of several species of Proteocephalus, and Bothriocephalus, known to be carried by copepods. Allacanthochasmus appears only exceptionally in the more precocious minnow-devouring young white bass. When the young fish change from a plankton to a fish diet, Allacanthochasmus infestation occurs, acquired by eating minnows containing the encysted worms. In the adult fish Allacanthochasmus occurs practically alone, with only an occasional adolescent proteocephalid or bothriocephalid derived no doubt from copepods accidentally included in the diet.

We have taken Allacanthochasmus from the intestine of a number of other hosts, including *Perca flavescens, Stizostedion vitreum, Percina caprodes zebra, Esox niger, Micropterus salmoides, Ameiurus nebulosus* and *A. natalis,* but in no instance were these worms mature. They were all small, recently excysted specimens. It is evident from our experience that Allacanthochasmus is highly specific for a single host, in Oneida Lake, *Lepibema chrysops*. In no other fish is it able to attain sexual maturity, but immature excysted worms may be found in any minnow-eating fish. Van Cleave found similar conditions in his original work on the species in the Mississippi Valley and the Great Lakes. However, Mr. S. H. Hopkins has collected specimens of what seems to be *A. varius* from the sheepshead (*Aplodinotus grunniens*) of the Pistakee Lake in northern Illinois. Though Adams and Hankinson have included the sheepshead as a fish which might be found in Oneida Lake, we have never taken it here.

The adult white bass in Oneida Lake seems to be limited in distribution. Most catches are made in Billington Bay. Hence all of our specimens of adult Allacanthochasmus are from this location. The immature specimens from the gut of other fish, however, have been taken in a variety of locations around the lake. Whether this indicates a general distribution of the white bass, or migratory movements of infested minnows, remains undetermined.

The adults and metacercariae of Allacanthochasmus are the only stages known in the life history.

Genus Apophallus Lühe, 1909

The genus Apophallus belongs to the subfamily Heterophyinae. In so far as known its members attain sexual maturity in the digestive tract of mammals and of birds. Price (1931) has recently reviewed this genus. The two American species which he mentions (*A. brevis* and *A. crami*) are distinctly different from the species which the present writers named *A. americanus*. For a detailed characterization of this form from Oneida Lake the reader is referred to Part I of this report (1932).

Apophallus americanus Van Cleave and Mueller, 1932

Hosts.—Immature in intestine of *Stizostedion vitreum*, and *Perca flavescens*; definitive host unknown.

Two accidental records of the occurrence of this parasite form our only basis for its inclusion in this survey. A single immature specimen was taken from a pike perch caught in a gill net set at a depth of fifty feet, near Cleveland, on July 15, 1930. A second single specimen was found in a yellow perch taken in Lower South Bay on January 21, 1931. It is highly probable that minnows or other small fish serve as normal hosts to the larvae of *A. americanus* and that the metacercariae reach maturity when the minnow is eaten by a suitable mammal or bird. The perch and pike perch are doubtless *culs-de-sac* in the life of the parasite. Since both *A. brevis* and *A. crami* reach maturity in gulls it is probable that *A. americanus* likewise finds its normal host in a water bird.

Family Microphallidae

In 1920 Travassos recognized the Microphallinae of Ward as a group which should be elevated to family rank. Prior to that date, and even since then, there has been great diversity of opinion relative to the disposal of the genus Microphallus in the taxonomic scheme. The history of this controversy is set forth in Part II, Section IV, of this series of publications, (1932). The present writers agree with Travassos in recognition of the Microphallidae as a distinct family based upon the concept of the genus Microphallus. At present the state of knowledge concerning other genera, i.e., Levinseniella, Spelotrema, Spelophallus, Monocaecum, and Maritrema, which from time to time have been assigned to the Microphallidae is still somewhat indefinite.

In Part I of this report Van Cleave and Mueller (1932) published two new species of Microphallus which they named *M. obstipus*, and *M. medius*. Mueller (1934) has subsequently removed these species to the related genus Maritrema. What was taken to be a seminal vesicle in the original account is in reality a cirrus sac. The cirrus sac is lacking in Microphallus, but is present in the related genus Maritrema, in which it lies transversely, anterior to the acetabulum, as in our specimens. Maritrema occurs in the adult stage in aquatic birds. Our specimens were immature, taken from the intestine of fishes.

Genus Microphallus Ward, 1901

Medium sized worms with pear-shaped spineless body. Alimentary canal limited to anterior third or half of body, consisting of prepharynx, pharynx, esophagus, and crura—of which the last are very short. Ovary spherical, dextral, para-acetabular, pretesticular. Testes two, lateral. Vitellaria composed of a few massive follicles. Receptaculum seminis lacking. Seminal vesicle pyriform, with large prostate gland. Genital pore at left edge of acetabulum. Small conical copulatory apparatus developed about terminus of ductus ejaculatorius. Cirrus sac lacking. Excretory bladder V-shaped. Adults in intestine of fishes. *M. opacus* and *M. ovatus* are represented by fully mature worms from the intestine of fishes.

The two species of Microphallus recorded in this study have been found in the rock bass of Oneida Lake, though that host has not been previously reported as a host of Microphallus in other waters.

Microphallus opacus (Ward, 1894)

Text Figure 6, Figure 1

Hosts.—*Ameiurus nebulosus* and *Ambloplites rupestris*, in intestine.

This species, which in part of its range seems to have wide limits of adaptability to the host, seems uncommon in Oneida Lake. *Amia calva*, the host from which it was originally reported, is either wanting or rare in Oneida Lake, and other fish recorded as hosts have been negative for *M. opacus* in the region studied. From the available records, it would seem that this species finds optimum conditions in Amia of the Great Lakes and upper Mississippi River, but has become firmly established in bullheads and some other fishes in some of the northern lakes.

We have only three specimens of this worm, two from a single *Ambloplites rupestris* and one from *Ameiurus nebulosus*. These worms are small, about 1.5 mm. in length, pronouncedly pear-shaped, with pointed anterior and broadly rounded posterior extremities. In one specimen from the rock bass, only a single cecum is present, suggesting the condition found in *M. ovatus*. Some characters of the two species intergrade to such an extent that it is difficult to make a positive differentiation in occasional specimens. The uterus tends to be bulkier and the vitelline follicles are gathered into a more compact cluster than in *M. ovatus*. The rock bass was taken off shore near Cleveland, the bullhead in Old Man Bay.

Crayfishes carry the metacercariae of this species in the liver (Ward, 1894).

Microphallus ovatus Osborn, 1919

Text Figure 6, Figure 2

Hosts.—*Esox niger* and *Ambloplites rupestris*. In intestine.

The small-mouth black bass, from which Osborn took the types of *M. ovatus*, is entirely free from this parasite in Oneida Lake. In as much as Osborn records infestations in Lake Chautauqua, N. Y., during summer months, the absence of this parasite from the black bass in Oneida Lake could not be explained on the ground of seasonal periodicity.

We have only two records of this species, one from a rock bass and one from a pickerel. The rock bass, from the vicinity of Brewerton, had three worms; the pickerel, from Ice House Bay, had eighteen. The pickerel had in its stomach a crayfish, from which we removed many cysts of the worm.

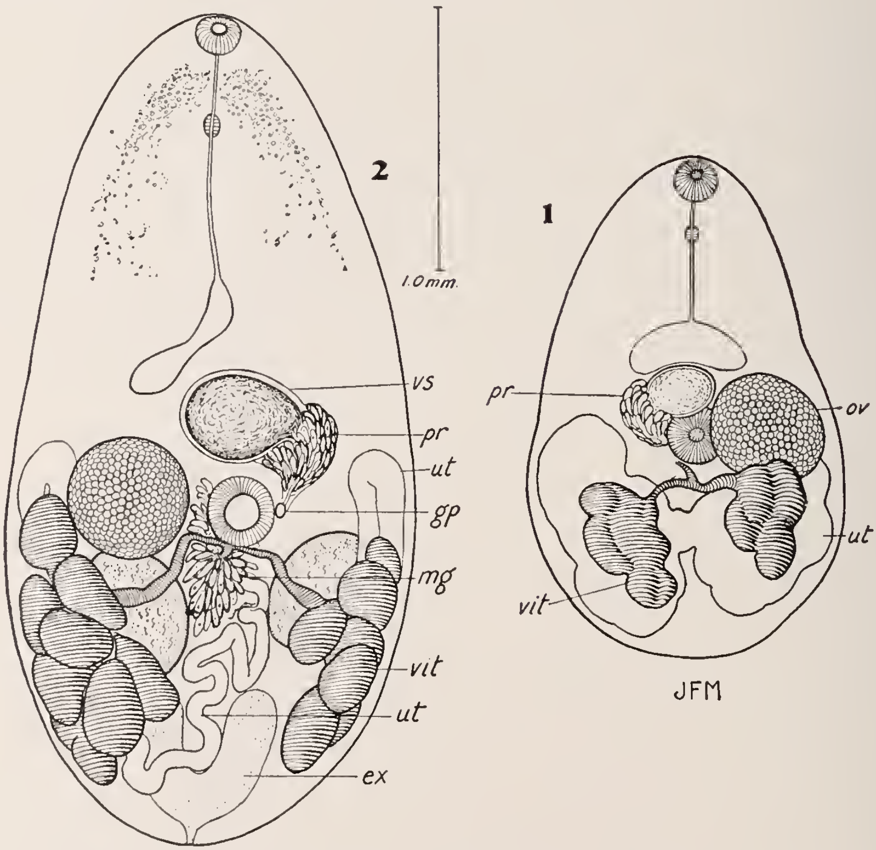


Fig. 6. Microphallus. 1, *M. opacus*, dorsal view of an imperfectly cleared whole mount. 2, *M. ovatus*, ventral view. (Same scale.)

ex—excretory bladder, gp—genital pore, mg—Mehlis' gland, ov—ovary, pr—prostate, ut—uterus, vit—vitellaria, vs—seminal vesicle.

This worm is the largest member of the genus, attaining a length of almost 3 mm. The form is much more slender and elongate than *M. opacus,* and not quite so pointed anteriorly. The easiest mark of recognition lies in the intestine, which usually forms a simple triangular sac at the end of the long slender esophagus. At times this sac is elongated obliquely to form a single cecum, and rarely the beginning of a second cecum is present. The worms in life have a dead white color.

The resemblance of *M. opacus* and *M. ovatus* is rather close. Moreover, what differences exist are largely bridged by variations. It seems not impossible that a comprehensive study of these forms might show them to be different modifications of the same species induced by the host relationship or other factors. In fact, a few of our specimens possess such clearly intermediate characteristics that positive determination was impossible.

According to Osborn (1919), the metacercaria of *M. ovatus* is found in the liver of crayfishes, in this respect also resembling *M. opacus.* Other steps in the life cycle are unknown.

Genus Maritrema Nicoll, 1907

This genus is similar in structure to Microphallus, but possesses a cirrus sac. They are small worms, with spinose skin. Pharynx and esophagus present, intestinal crura short. Excretory bladder V-shaped. Genital pore at left of acetabulum, with a long cirrus sac lying transversely anterior to acetabulum. Ovary right, on posterior edge of acetabulum, testes lateral. Vitellaria variously distributed within a band passing transversely across body posterior to acetabulum, and around posterior border of body. Uterus winding, filling posterior portion of body.

Normally found in intestine of wading birds and in mammals. Our specimens immature, from gut of fishes, in which they were no doubt introduced along with the intermediate host, probably a crayfish.

Maritrema obstipum (Van Cleave and Mueller, 1932)

Host.—*Ambloplites rupestris.* In intestine.

This species was described in our first paper of this study under the name *Microphallus obstipus.* It was removed to Maritrema by Mueller (1934). We found only a single specimen, which is now deposited as type of the species in the United States National Museum. This was an immature worm in that it contained no eggs as yet, but had the reproductive organs otherwise fully developed. The host was a small rock bass caught in Fairchild Bay, July 20, 1929.

Dr. E. W. Price of the United States Bureau of Animal Industry mentions in a private communication that he has adults of either this or a closely related worm from two rodent hosts.

Maritrema medium (Van Cleave and Mueller, 1932)

Hosts.—*Perca flavescens* and *Ambloplites rupestris.* In intestine; some enclosed in cysts.

This species was likewise named and fully described in our earlier paper of this series, and like the above species first placed in the genus Microphallus, and later removed to Maritrema. At that time we had only a single specimen of the worm, which we placed in the United States National Museum as type. Subsequently we have found ten other specimens. These are all minute, immature forms, either enclosed in a tough clear cyst wall, or recently excysted. Doubtless this species reaches maturity in some other host and its presence in the intestine of fishes is to be regarded as an accident. It probably lies encysted in crayfishes, or some other small aquatic animal which is eaten both by fish and the true definitive host—probably a fish-eating mammal or bird.

We have taken this worm four times—on three different occasions from the yellow perch, and once from the rock bass. In three of these instances only a single specimen was encountered. From one perch, however, eight specimens were secured. Two of the perch were taken in Short Point Bay, August 29, 1929. The other was taken through the ice in Big Bay, December 27, 1930. The rock bass came from Fairchild Bay, July 20, 1929. Two crayfishes were found in the stomach of one perch from which the eight worms were obtained. These crayfish were partly digested and very possibly the worms may have come from them. Crayfish are known to act as the intermediate host to the genus Microphallus, but nothing is known with certainty about the life history, or definitive hosts of our species of Maritrema.

Some of our specimens of *M. medium* show a condition of the oral sucker, pharynx, and esophagus intermediate between *M. medium* and *M. obstipum*. However, we have never observed any intermediate condition of the vitellaria. Possibly the two species are synonymous.

Family Clinostomidae

The family Clinostomidae was recognized by Lühe to include as type the genus Clinostomum which Leidy named in 1856. This family has been acknowledged by many subsequent authorities, including Poche (1926). The genus Clinostomum is the only representative of the family so far recognized in the Oneida Lake survey.

Genus Clinostomum Leidy, 1856

Worms of the genus Clinostomum are found in the larval state as small whitish grubs encysted in the muscles and beneath the skin of fishes and frogs, and as adults are found in the mouth, under the tongue, and in the throat and esophagus of fish-eating birds such as herons, bitterns, etc. The form found in fish is from 4 mm. to 5 mm. in length and about 2 mm. in width. It usually lies near or just beneath the skin, especially at the base of the fins and tail. In such locations it forms bulging wart-like protuberances on the surface of the fish, which then are spoken of as "grubby" by anglers. The cysts of Clinostomum, in a heavy infestation, may be abundant in other locations such as the abdominal wall, beneath the peritoneum, in the general musculature, in the membranes of the head, throat, and gills, in the gill filaments and even in the conjunctival sac. These worms are of considerable economic importance, for in many regions fish carry such a heavy infestation of these grubs as to be rejected as human food. Although there is no danger of the worm infesting human beings, even if swallowed alive, there is naturally a strong prejudice against eating fish thus parasitized. The living worms when squeezed from the cyst are very active. They have a peculiarly opaque, brilliant white color. The sides are more or less parallel and the body is flattened. In the heron, the adult worm has a darker, frequently reddish color. To some extent at least the adult worm sucks the blood of the bird host, and evidently some of the hemoglobin is absorbed into its own body tissues, imparting the reddish color. The parasite frequently lies beneath the tongue of the bird and has a most tenacious hold upon the mucous membrane. So tightly do the worms adhere that it is almost as though they had grown to the surface. Their flattened bodies offer little resistance to food swallowed by the bird and thus reduce to a minimum the possibility of being dislodged. For this firm attachment the worm is excellently equipped. The acetabulum is large and powerful. The oral sucker is small, but this feature has been compensated by a specialization of the forebody. The entire anterior tip, with the oral sucker in the middle, has become flattened and its margin produced into a sharply defined collar or lip. This area is usually slightly concave with the oral sucker rising in the center on a small conical elevation. The entire anterior region or "oral field" is used as a sucker by the worm in anchoring itself in the upper alimentary tract of the bird. (See text figure 7.)

In addition to the form which occurs encysted in fish, other worms of this same genus occupy cysts in the tissues of frogs. Both of these types have been encountered in the Oneida Lake area. There has been some controversy over the specific name of the Clinostomum living in fishes, but most recent workers agree that this form is the *C. marginatum* described by Rudolphi in 1819.

Cort, 1913, separated the forms from the fish and from the frog, giving the latter form the name *C. attenuatum.* He adduces as evidence for separation of the two the following points: the location of the cyst in the host, the position of the worm in the cyst, the proportions and topography of the body—especially the difference in the forward limits of the uterine sac, and the relative size of the spines. *C. attenuatum* is thin and ribbon-like, and the sides of the body are parallel, the width being uniform throughout. *C. marginatum,* on the other hand has a thicker body, with a strongly arched dorsal surface, and there is a marked constriction at the level of the acetabulum. And finally, the spines of *C. attenuatum* are much coarser than those of *C. marginatum.*

The great blue heron is perhaps the commonest host of the adult *Clinostomum marginatum.* Cort was inclined to regard the bittern as the host of *C. attenuatum.* As support for this view he cites the similarity between Clinostomum described from the bittern by Wright, 1879, and the larval *C. attenuatum.* We have numerous Clinostomum from the great blue heron, *Ardea herodias,* and these as a group are recognizable as *marginatum.* We have also three Clinostomum from the bittern. Two specimens are immature, but possess the characters of *marginatum.* The third worm is mature and of the *attenuatum* type. It would seem therefore that *C. marginatum* occasionally infests bitterns, but whether or not it is able to reach maturity in this host is not brought out by facts at present available. Alvey and Stunkard (1932:174) have recently recorded the occurrence of *C. attenuatum* in the great blue heron. Thus it would seem that neither species is specific in its host relationships.

Clinostomum marginatum (Rudolphi, 1819)

Text Figure 7, Figures 1–3

Hosts.—Immature in cysts in *Perca flavescens, Micropterus salmoides, Pimephales promelas, Catostomus commersounii, Ambloplites rupestris* and *Eupomotis gibbosus*. Adult in mouth, throat and esophagus of *Ardea herodias*.

While several fishes are here listed as harboring the larvae of this parasite, by far the commonest host is *Perca flavescens*. From the other hosts we have usually only single infestation records. The record from *Pimephales promelas* is on the basis of three fish which were caught in the Colvin Street ponds near the Forestry College in Syracuse. These fish were taken in the spring of 1929 and kept in class room aquaria. The infestation was first noticed in December and January, 1929-1930. On January 14, 1930, one fish was operated upon and the cysts removed, whereupon it was returned to the tank. All snails had previously been removed from the aquarium so that it was unfortunately not possible to tell whether the fish had become infested in the aquarium (which seems most likely) or whether they already carried the parasites when collected in the field. They were quite normal in appearance when placed in the tank and did not develop the nodules indicative of Clinostomum until about eight months later. No record had been kept of the snails which were in the tank, so the opportunity of tracing the life history was lost. With the exception of this host all of our other records are from Oneida Lake or nearby waters. The list of localities is as follows: west shore of Walnut Point; Shepherd's Point; Poddygut Bay; Short Point Bay; Old Man Bay; Cleveland Harbor; Mill Pond, Cleveland. All of these localities are shallow, shore-water situations. Not a single Clinostomum-infested fish was taken in the deep water. In the perch, which inhabits both deep and shallow water, the infestation was exclusively limited to those taken in shallow water. The infestation of perch with this parasite is so much heavier and more frequent than that of other fish, that it is chiefly this host which must be discussed in connection with the ecology of the parasite. *Clinostomum marginatum* is in no way limited to the perch as a second intermediate host. It can infest nearly all species of scale fish, it would appear, but in view of what has just been said, hosts other than perch can be dismissed as of very slight or merely accidental importance. The locality of highest incidence in the entire lake is the west shore of Walnut Point. We found the perch from this spot practically without exception infested with Clinostomum, and the numbers in individual fish were relatively enormous. For example, in two perch specimens the total numbers found were respectively 191 and 325. The count for one of these fish by anatomical regions was as follows: caudal peduncle, 33 cysts; head, throat, gills, 70 cysts; body wall, peritoneum, 32 cysts; general musculature, 56 cysts.

In no other locality were such mass infestations encountered. This fact was made more striking by contrast, for even nearby localities showed an abrupt difference in incidence of the infestation. A submerged, shallow, trough-like depression extends westward from Walnut Point between a rocky bar and the south shore of the lake. The bottom of this trough is mostly of clean material—sand and gravel, and supports a variety of mollusk life. It is probable that the intermediate mollusk host of Clinostomum is a species which finds conditions unusually favorable in this habitat and hence exists here in large numbers and spreads Clinostomum infestation among fishes. Only one of the perch taken from this locality was free of Clinostomum. This was an eight-inch specimen harboring no parasites of any kind. We have also found some heavy infestations of perch in Short Point Bay, where the bottom is very similar to that found at Walnut Point.

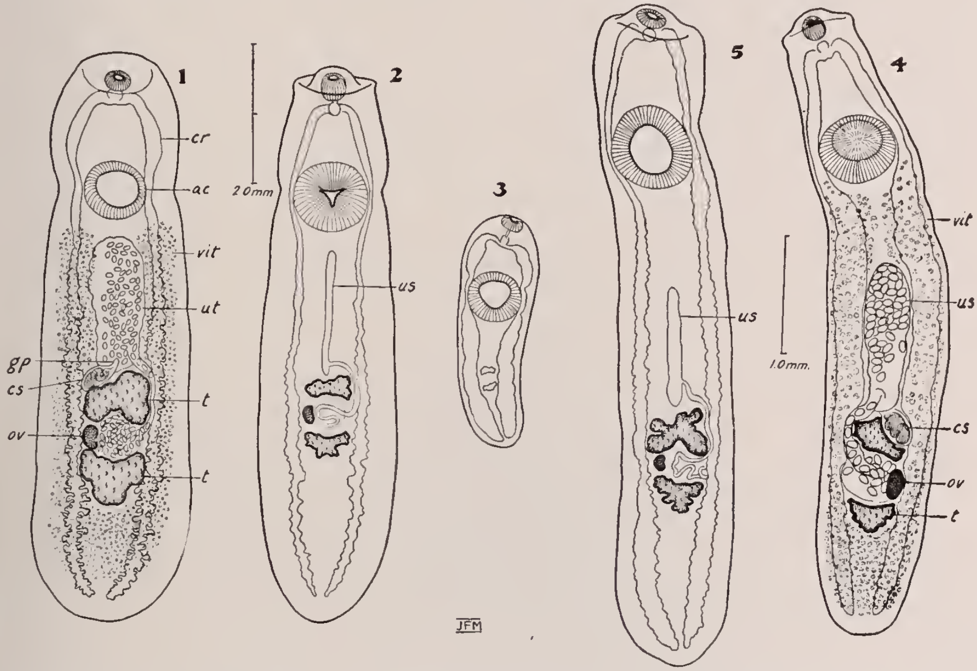


Fig. 7. Clinostomum. (Scale with 2 applies to 1–3.) 1, *C. marginatum,* adult from blue heron. 2, *C. marginatum,* metacercaria from the yellow perch. 3, *C. marginatum* ?, metacercaria from *Pimephales promelas.* 4, *C. attenuatum,* adult from the bittern. 5, *C. attenuatum,* metacercaria from the green frog, same scale as 4.

ac—acetabulum, cr—crura, cs—cirrus sac, gp—genital pore, ov—ovary, t—testes, us—uterine sac, ut—uterus, vit—vitellaria.

The western end of the lake is most frequented by herons and it was from localities at this end that we got our heaviest Clinostomum infestations. However, the unusually heavy infestation with Clinostomum found at Walnut Point can only be explained on the ground that in this locality the intermediate host is unusually abundant, and that conditions here generally promote the infestation.

Our collections at Walnut Point were all made during the summer of 1929. Since that date drought, with resulting low water, has caused considerable change in the fauna of some of the shallow water localities in the lake. Localities once extremely rich in invertebrate life, such as the flats off Wantry and Long islands, were almost sterile in succeeding summers. Whether such changes have in any way affected the Clinostomum infestation at Walnut Point we do not know, since we have made no further collections there.

All of our records of Clinostomum infestation, except the unique record from aquarium specimens of *Pimephales promelas,* were for the summer. With the exception of three, all of these were made during the month of August, 1929.

Thus in this single month we have comparative data on all of the habitats at the western end of the lake. The infested common sucker was taken in the Mill Pond, Cleveland, July 8, 1931, while the rock bass was taken in Cleveland Harbor, August 26, 1931. *Pimephales promelas* developed its infestation in December, 1929, but having been kept in an aquarium, was living under unnatural conditions and possibly acquired its infestation from mollusks kept in the same aquarium. Clinostomum leaves the fish at the end of the summer, so that fish caught in the winter are free of the grubs. In Oneida Lake the infestation reaches its height during the month of August, and after this period subsides. The lake reaches its highest temperature about the middle of July. Apparently, it is just at this time that Clinostomum infestation in the fish sets in, and within a month the fish have acquired the knotty swellings associated with the condition. We do not know how the Clinostomum larvae enter the fish, or how they are lost in the fall. Cysts near the surface are so easily ruptured that frequently the worms burst forth on mere handling of the host. It is possible that in the fall the cysts automatically burst, shedding the worms, to their destruction.

In spite of the economic loss entailed by Clinostomum through rendering the infested fish unfit for human food, we have found no evidence of host mortality due to the parasite. Even the most heavily infested perch, extremely unsightly, were active and seemed to suffer no inconvenience from the infestation.

Infested birds were taken at various points near the west end of Oneida Lake during the summer of 1928. No birds from other areas were examined, hence the lack of records from other parts of the lake does not indicate lack of infestation. The freedom with which the water-birds move about when feeding would exclude any possibility of rigid restriction of areas of infestation within the lake. Herons leave the Oneida Lake region during the fall for their southward migration. The latest examination in our records for the great blue heron was September 12, 1928. This bird contained *C. marginatum*, and it is probable that infestations are carried throughout the winter. The migratory habits of the herons explain the wide geographical distribution of *C. marginatum*, for it occurs generally throughout North and South America. It is not improbable that various species of mollusks throughout the range of the herons serve as hosts to the larval worms, and expose the fish, and through them the herons, to continual reinfestation.

The first publication of the New York State College of Forestry in its technical series was a preliminary report by Smallwood (1914) on Clinostomum in fishes of certain Adirondack ponds. In spite of the fact that several investigators have given attention to this species, the details of the life history are unknown.

Clinostomum attenuatum Cort, 1913

Text Figure 7, Figures 4–5

Hosts.—Immature cysts in *Rana clamitans*. Adult in *Botaurus lentiginosus*, mouth, throat, and esophagus.

This species is included here solely for comparison with *C. marginatum*. Since the larvae do not occur in fishes we have made only incidental observations on them. The two green frogs examined by us were from the vicinity of Rome, N. Y. Comparison of this material with our fish Clinostomum convinced us of the validity of the species *C. attenuatum*.

Family Sanguinicolidae

In Poche's extensive treatise on the classification of the flatworms (1926), the genus Sanguinicola is recognized as the type and only inclusion of the family Sanguinicolidae. In habitat the members of this family are restricted to the blood system of fishes. Other blood flukes living in turtles (Spirorchidae and Aporocotylidae) are joined with the Sanguinicolidae to form a superfamily to which Poche (1926:175) has ascribed the name Sanguinicolida. This necessity of a distinct superfamily to include the blood flukes of cold-blooded vertebrates indicates that these forms do not represent fortuitous adaptations on the part of flukes characteristically adjusted to life in other organs or normal to other vertebrate hosts. They constitute a natural group showing intimate modifications from the stereotyped plan of trematode structure.

In the Oneida Lake survey only the type genus of this family has been found, attention having been directed almost exclusively to the parasites of fishes.

Genus Sanguinicola Plehn, 1905

In 1905 Miss Plehn described some small worms which she encountered in the blood of fishes and placed them in the Turbellaria. It was later shown that these worms belong to the trematodes. No member of this genus had ever been recorded from North America until the present writers described *S. occidentalis* in Part I of this report. No other species has been reported from this continent.

In the original description of *S. occidentalis,* attention was directed to the fact that larvae from St. Louis, Mo., described by McCoy (1929:199), seem to be larvae of Sanguinicola, but no additional information on this point is available, and the matters of distribution and speciation of the genus in North American fishes remain wholly undetermined.

Sanguinicola occidentalis Van Cleave and Mueller, 1932

Host.—*Stizostedion vitreum.* In heart and blood vessels.

We have five records of infestation with this worm, all from *Stizostedion vitreum.* Two of these records are for collective examinations. The pike perch is evidently the sole host in Oneida Lake. We have examined numbers of yellow perch, but in no case was an infestation with Sanguinicola found. The numbers found in infested pike perch vary. The largest number found was 12. These were taken from the heart and conus of a young Stizostedion, only five inches long, taken in the trawl one and one-half miles off Jewell. This is an isolated instance, but may indicate a heavier infestation of the young pike perch than of the old. This was the only pike perch of such small size examined, since the young are seldom taken. In large infested fish usually a single worm was found, or at most two or three.

The incidence of infestation is low, probably not more than ten per cent. Infested fish were taken in various localities in deep water. The pike perch during most of the year is a deep-water resident, migrating shoreward and up creeks in the early spring to spawn. It is undetermined where the infestation is acquired.

In this country McCoy (1929:199) has described a cercaria of the Sanguinicola type in Missouri. Possibly this is the young of our species. However, nothing definite is known of the life history of this worm.

A somewhat similar cercaria has been described by Croft (1933), *Cercaria whitentoni*, from the vicinity of Stillwater, Oklahoma. This suggests that there may be additional species of Sanguinicola in fishes of this continent.

Scheuring (1922), Ejsmont (1925) and others have worked out the life cycle of European species of this genus. In the case of the European types the eggs penetrate the tissues and escape to the outside through the gills or the kidneys. We have examined pike perch for evidences of injury or degeneration which might be attributed to infestation with Sanguinicola, but with negative results.

Family Strigeidae

The strigeids, or holostomes as they are called in much of the literature, constitute a family of digenetic trematodes, individuals of which reach maturity chiefly in birds and mammals. The adult worm is strikingly unlike the metacercaria and for that reason the larval stages when encountered defy assignment to their respective genera. In consequence, parasitologists have followed the custom of classifying the metacercariae when discovered and of assigning names to what seem like closely allied forms. These names are treated as the equivalent of generic groups, but as the life histories of individual species are determined the species within these groups of convenience are reassigned to their respective genera. Since fishes very commonly act in the capacity of host to strigeids, this family demands especial consideration in the present report.

In the large body of literature on Strigeidae of North America, the works of LaRue and his associates stand out prominently. Since 1926, twenty-four papers on the Strigeidae alone have come from the University of Michigan laboratory where LaRue is directing an intensive study on the morphology and life cycles of members of this family.

In the survey which we have conducted large numbers of metacercariae of Strigeidae have been found. These belong to three distinctive types recognized as Diplostomulum, Tetracotyle, and Neascus.

Each type has a more or less definite location in the host. Thus Diplostomulum is usually, and in the case of our material always, found in the eye,—in either the anterior or posterior chambers, or both, or in the lens itself. The worm is found free in the eye humors, or burrowing in the lens substance. It is never surrounded by a cyst. Tetracotyle is found encysted in the muscles, mesenteries, or pericardium of the host, and is surrounded by a rounded, usually thick, cyst. Neascus has an ovate, thin cyst, and is found on the viscera or mesenteries, in the skin, and frequently in the pericardium.

All of these types may occasionally be taken from an ectopic location, such as the alimentary canal of game fishes, into which they are introduced along with the original host when the latter falls prey to a carnivorous fish. Such a location (i.e. —alimentary canal) can not be regarded as normal for these larvae.

For the most part, the species of holostomes hitherto described have been named from the larval stages. The life histories and adults are to a great extent unknown or unrecognized as yet. The problem is complicated by the fact that experimental work has demonstrated that morphologically similar larval forms are not always identical. LaRue, for instance, has shown that *Diplostomulum huronense* from *Percopsis omisco-maycus,* morphologically indistinguishable from the Diplostomulum from the perch eye, is not the same as this latter form. *Diplostomulum huronense* from the eyes of the trout perch was found by feeding experiments to be the young of *Diplostomum huronense,* a parasite of the herring gull, *Larus argentatus.* However, the morphologically similar larva from the eyes of the yellow perch, when fed to gulls, failed to develop. This latter therefore must be the young of a different worm.

It is the usual procedure in handling holostomes to give the living worms careful microscopic study. Under the conditions incident to our work we found this impossible at times. The mass of material encountered in the field was too great and facilities too poor to permit detailed examination of the living holostomes. Nearly all of the material was fixed at once and preserved for future study. The structure of the excretory bladder, and certain other diagnostic features can be made out best in living material. The natural shape of the worms suffers some alteration due to contraction at the moment of fixation. In general, the effect of fixation is to obscure natural differences in the various forms, and to impress upon all a more or less uniform appearance. All of our studies have been made on fixed and stained material, supplemented by a few superficial notes taken from the living material in the field.

In our collections, Diplostomulum is the most abundant type, and after this come Tetracotyle and Neascus. These groups will be discussed individually with reference to host records and incidence.

The group Diplostomulum is a larval genus including small, flattened and usually slightly elongate agamodistomes. The worms are usually found in the eyes of fishes, and are without a cyst or capsule. The body is not clearly divided into two regions although a small caudal lobe is present. Oral sucker and pharynx are present, also two lateral suckers or cotylae, which vary in state of contraction and degree of development. A small acetabulum occurs some distance behind the midpoint, followed by a large adhesive or "holdfast" organ. The adhesive organ usually has at its posterior edge a small transverse structure known as the "holdfast" gland. In the caudal lobe are found the excretory bladder and the primordia of the gonads. The excretory bladder has a median longitudinal septum, and sends off fine anterior branches which ramify throughout the body of the worm. The alimentary canal has an esophagus of varying length. The crura usually extend into the caudal lobe, overlapping the excretory bladder.

Two of the diplostomulids which we frequently encountered have been tied up with the adult forms, and are therefore treated below under their proper adult genus, Diplostomum. In the case of others the adult has not yet been recognized, and these are accordingly treated under the larval genus Diplostomulum. We are unable to identify all of our diplostomulids with certainty. Where possible we discuss these as species and treat the remainder as host groups.

Adult Genus Diplostomum Von Nordmann, 1832

Diplostomum flexicaudum (Cort and Brooks, 1928)

Plate 31, Figure 4

Synonyms: *Diplostomulum gigas* Hughes and Berkhout, 1929; *Cercaria flexicauda* Cort and Brooks, 1928.

Larval Hosts.—*Catostomus commersonnii.* In lens of eye.

In 1929 Hughes and Berkhout described a metacercaria occurring exclusively in the lens of the common sucker (*Catostomus commersonnii*), which they named *Diplostomulum gigas.* Van Haitsma (1931a) made an intensive study of the life history of this form and discovered that it develops from *Cercaria flexicauda* Cort and Brooks, 1928, and further found that the adult belongs to the trematode genus Diplostomum. Consequently, according to priority, the name of this species becomes *Diplostomum flexicaudum* (Cort and Brooks, 1928). Through feeding experiments Van Haitsma determined the entire life cycle of this worm, and found that it reaches maturity in the intestine of gulls. Quoting Van Haitsma (1931a: 511), "Eggs in the feces of the herring-gull are deposited in water. From these eggs miracidia hatch in about three weeks. After escaping from the eggs the miracidia penetrate *Stagnicola emarginata angulata* (Sowerby) and probably other snails, within a few hours. Inside the snails, the miracidia transform into mother sporocysts which in turn produce daughter sporocysts. Within the latter, cercariæ develop about six weeks after the penetration of the miracidium into the snail. The cercariæ escape from the snails and lead a free-swimming life for less than a day. They penetrate various parts of the body of the common sucker and travel to the eyes of these fish, finally coming to rest within the lens capsule, where they grow and metamorphose into the diplostomulum stage. It probably takes about five or six weeks from the time the cercaria penetrates into the fish before the diplostomulum has reached the infesting stage. When common suckers then are eaten by herring gulls the diplostomulum attains sexual maturity in the intestines of these birds in less than one week."

The effects of the diplostomulids on the fishes are apparently very severe. Van Haitsma (1931a:508) states, "There is no doubt that the penetration of large numbers of the cercariæ of *D. flexicaudum* (Cort and Brooks) into both species of suckers of the two experiments last described was the cause of the death of these fishes." The same author further attributes wholesale destruction of fish to this same cause—holostome penetration. He concludes that "...... the cercariæ of *D. flexicaudum* cause the death of a large proportion of the thousands of fishes which are found on the shores of Douglas Lake every summer." Since diplostomulids are not specific in the fishes attacked, even though there may be fairly well established limits to the host species capable of inducing normal development of the metacercariæ, death not only of suckers but of numerous other species may be attributable to penetration by larvae of *Diplostomum flexicaudum.*

In view of the excellent description of this form given by the original authors, a detailed treatment here is uncalled for. The presumption is justified that our diplostomulids from the eyes of *Catostomus commersonnii* are in all probability the larvae of *Diplostomum flexicaudum.* Our worms were found exclusively in the lens, as is true of this species. There are, however, some differences between Hughes and Berkhout's account of *Diplostomulum gigas* and the present material. *D. flexicaudum* (*D. gigas*) as figured by Hughes and Berkhout is heart-shaped. Our specimens are of more slender proportions and the acetabulum and other posterior structures are farther caudad. In life, however, our worms more nearly corresponded to the shape given for *D. flexicaudum.* At death the fixation causes a narrowing and elongation. The anatomy of our worms in other respects corresponds to the original description.

The length is given by the original authors as averaging 0.417 mm. (minimum 0.375 mm., maximum 0.465 mm.). The average width is given as 0.302 mm. Our specimens vary in length from 0.390 mm. to 0.600 mm., with an average width of a little more than one-third the length.

Diplostomum huronense (Hughes and Hall, 1929)

Synonym: *Diplostomulum huronense* Hughes and Hall, 1929.

Plate 31, Figures 5–7

Larval Host.—*Percopsis omisco-maycus* (and possibly *Perca flavescens*), in humors of eyes.

Diplostomulum huronense was described by Hughes and Hall, 1929, from the eye of the trout perch, Douglas Lake, Mich. The parasites occurred chiefly in the chambers of the eyeball; ". . . less than nine per cent of the worms occurred within the lenses". The finding of a diplostomulid of the same habits from the same host in Oneida Lake is presumptive evidence that *Diplostomulum huronense* occurs also in our collections. A comparison of this material with the description of Hughes and Hall and with their figure, brings out certain discrepancies.

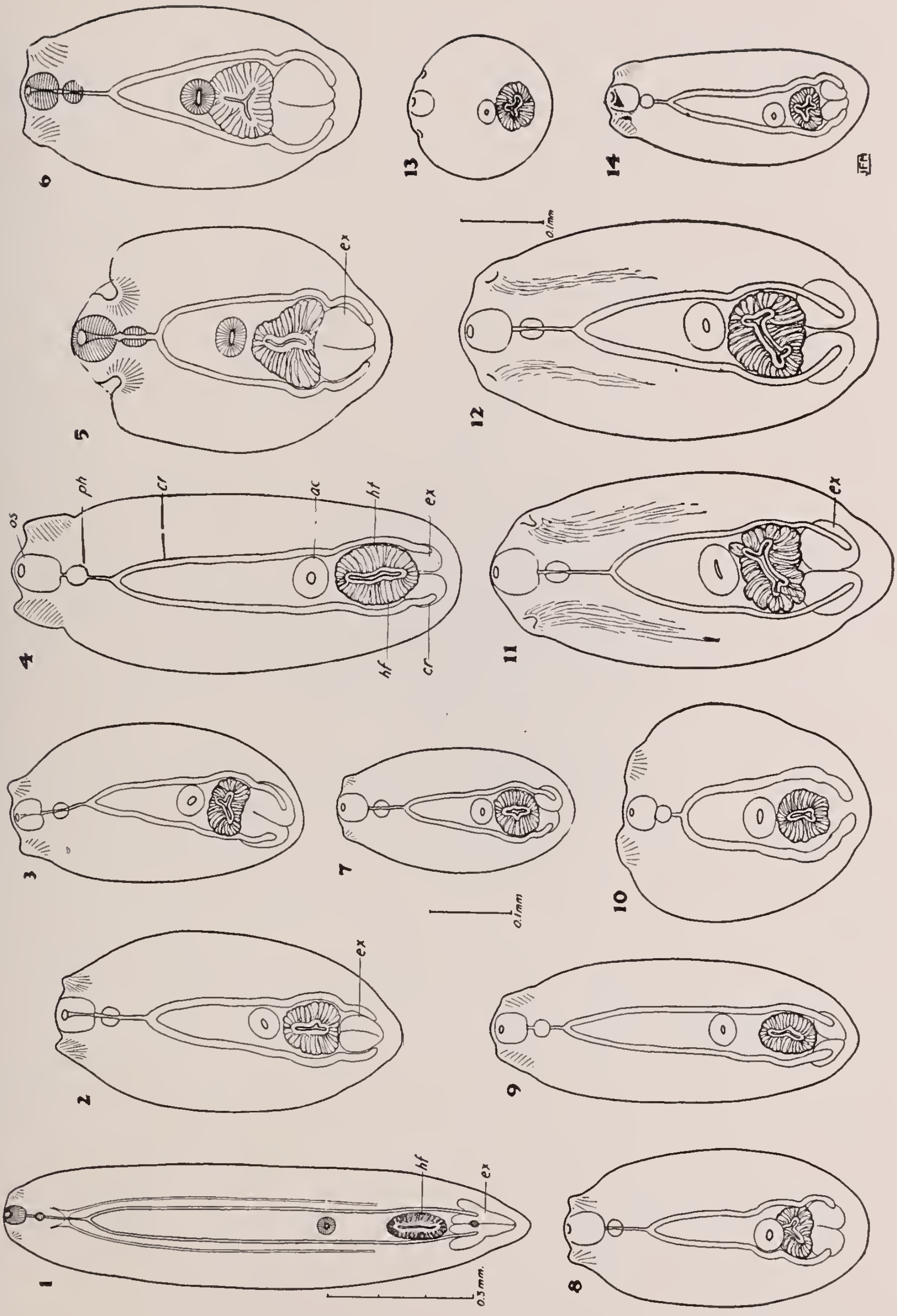
The average length of the diplostomulid preserved and mounted *in toto* is given by the above authors as 0.257 mm., with extremes of 0.226 mm. and 0.317 mm. The average length of our specimens is about 0.255 mm., and the largest measurement about 0.300 mm. This measurement thus agrees for the two forms, but in width there are obvious disparities. *D. huronense* is heart-shaped or ovoid as shown in the illustration by Hughes and Hall. In our material the worms are narrower and more elongate. Other differences which stand out are the position of the acetabulum—in Oneida Lake material definitely posterior to the middle of the body, in *D. huronense* anterior to the middle. The pharynx in *D. huronense* is represented as long and cylindrical, covering the entire distance from the oral sucker to the fork of the intestine. In worms under consideration, this organ is small and spherical with a definite prepharynx before it, and a definite esophagus behind. Also in our worms the lateral suckers are everted as muscular epaulets in the shoulder region, while in *D. huronense* they are represented as deeply invaginated sacs.

Hughes and Hall report that *D. huronense* is similar to a worm found in the vitreous humor of the yellow perch. "In this host (yellow perch) the worms were found exclusively in the vitreous humor. Although the diplostomulum found in the yellow perch is apparently morphologically identical with the one in the trout perch, the feeding experiments performed by LaRue (1927, p. 27) seem to indicate that the former is not the larva of *Diplostomum huronense.*"

Plate 31. Diplostomulum, various species. (Figs. 2–14 all drawn to same scale as that shown with Figs. 7 and 12.) 1, *D: scheuringi,* from the yellow perch. 2, *D*. sp., from the rock bass. 3, *D*. sp., from *Leucosomus corporalis.* 4, *D. flexicaudum,* from the common sucker. 5, 6, *D. huronense* (?), from the yellow perch. 7, *D. huronense,* from percopsis. 8, *D*. sp., from *A. natalis.* 9, *D*. sp., from *S. miurus.* 10, *D*. sp., from the eel. 11, *D*. sp., from Percina. 12, *D*. sp., from the white bass. 13, 14, *D*. sp., from Lota.

ac—acetabulum, cr—crura, ex—excretory bladder, hf—holdfast organ, os—oral sucker, ph—pharynx.

PLATE 31



We also have found these diplostomulids abundant in perch eyes. The worms from the perch, however, are of several different types. One of these, *Diplostomulum scheuringi*, is a different species altogether. The other type is smaller and evidently occurs in several different growth or contraction stages in our collections. The larger or more expanded of these resemble the worms taken from the trout-perch eye but are somewhat larger—the average being about 0.450 mm. long, with the largest about 0.510 mm. Others are smaller, but are nevertheless a little larger than *huronense* as reported by Hughes and Hall (0.345 mm. as compared with 0.257 mm.). In the smaller forms the pharynx has the relationships shown by Hughes and Hall for *huronense*, touching the oral sucker anteriad and the fork of the intestine posteriad. These small forms on our slides undergo a gradual transition to the condition of the larger forms from the perch eye, exclusive of *D. scheuringi*.

LaRue (1927, p. 27) demonstrated that *D. huronense* from the eyes of the trout perch, is the young *Diplostomum huronense*, parasitic in gulls; while the form from the eyes of the yellow perch failed to mature in gulls.

We conclude that we have *Diplostomulum huronense* from the eye of *Percopsis omisco-maycus*, and that we have the closely similar form from the eye of *Perca flavescens;* but like LaRue, and Hughes and Hall, we are unable to shed light on the identity or relationships of the latter worm.

Larval Genus Diplostomolum Brandes, 1892

Diplostomulum scheuringi Hughes, 1929

Plate 31, Figure 1

Hosts.—*Perca flavescens, Eupomotis gibbosus, Ambloplites rupestris, Percina caprodes zebra, Salmo fario, Pomoxis sparoides, Lota maculosa*, in humor of eyes.

This species was described by R. C. Hughes (1929) from the eyes of *A. rupestris, E. gibbosus*, and *P. flavesceus*, with the rock bass most heavily infested. This worm is at once recognizable by its size and proportions. It has a tongue-like shape with parallel sides. The anterior end is blunt and the posterior end pointed. The lateral suckers are, in the largest worms, vestigial. In addition to these characters, the esophagus is unusually long. The crura terminate in the caudal lobe near the posterior tip.

The above list shows that this species occurs in a variety of hosts. In all cases the worms are morphologically similar, however, and we are satisfied that a single species is represented. These worms range in length from about 0.750 mm. to 1.065 mm. The usual length, or mode, lies around 0.945 mm.

We at one time questioned the validity of *D. scheuringi*. We have found diplostomulids from the yellow perch representing a perfectly intergrading series from the *Diplostomulum huronense* (?) usually found in that host, to the *D. scheuringi* type occasionally present. Against the fact that such a series may be natural rests the manner in which *D. scheuringi* occurs. If our series were really a growth series one should expect at times to find a mass infestation with *D. scheuringi* comparable to the heavy infestations with *D. huronense* in perch, but such never occurs. We have pure infestations with *D. scheuringi* from *Lota maculosa* (host record 701 : 9 worms) ; *Ambloplites rupestris* (host record 668 : 75 worms) ; *Pomoxis sparoides* (host record 667 : 6 worms) ; *Eupomotis gibbosus* (host record 535 : 3 worms) ; *Salmo fario* (host record 563 : 2 worms). In some of these hosts *D. huronense* has never been found. The intermediate forms have been found only in perch and are very rare. We therefore reject our earlier view as to the identity of *D. huronense* and *D. scheuringi,* set forth in an abstract (Mueller and Van Cleave, 1931 : 126-127).

D. scheuringi occurs only in the humors of the eye—chiefly the vitreous humor—never in the lens.

Diplostomulum of Undetermined Species

We have a number of diplostomulids of uncertain identity, from various hosts as given below. Van Haitsma (1931a :509) has shown experimentally that Diplostomulum larvae are not specific in their tissue-penetrating propensities, but will bore their way into fishes other than the ones in which they normally develop. Many of the following instances are records of the occurrence of a few diplostomulids in the eyes of a host species, most individuals of which are free from the worms.

Diplostomulum sp. from *Percina caprodes zebra.*—A mixed infestation with Diplostomulum. One form, *D. scheuringi,* mentioned above. The other (Plate 31, Fig. 11) a smaller worm of about 0.480 mm. length. Probably from the humor of the eye. Of a broadly ellipsoidal shape. Oral sucker 0.064 mm. long by 0.048 mm. wide. Pharynx much smaller—0.028 mm. long by 0.020 mm. wide. Other characters shown in figure. Roughly similar to *Diplostomulum flexicaudum* and *D. huronense,* this worm nevertheless has a distinctive aspect. It is larger than *D. huronense,* but within the size range of *D. flexicaudum.* It differs from the latter, however, in the character of the intestine, and in possessing a much larger acetabulum. The acetabulum and holdfast organ are in close contact, which is not the case in *D. flexicaudum.* The cotylae are sometimes everted, sometimes withdrawn. Heavy muscular strands pass inward from them and continue within the worm toward the posterior end. Comparisons between this form and other species can best be made by consulting the drawings (Plate 31, Fig. 11).

Diplostomulum sp. from *Leucosomus corporalis.* Twenty specimens from lens. Small, 0.300 mm. to 0.390 mm. long. Shape (Plate 31, Fig. 3) elongate, width less than half the length. In general topography like *Diplostomulum flexicaudum* from lens of *Catostomus commersonnii.* Both hosts are rather close together in the taxonomic system, and the worms in each case were found in the lens. The form is within the size range of *D. flexicaudum.*

Diplostomulum sp. from *Ambloplites rupestris.*—Worms (Plate 31, Fig. 2) from posterior eye chamber. Similar to *D. huronense* from Percopsis and *D.* sp. from the yellow perch. In size they are intermediate between these two species—about 0.375 mm. long. Ellipsoidal, truncate anteriorly. Taken on only one occasion.

Diplostomulum sp. from *Lota maculosa.*—We have found two types of diplostomulids in the eye of this host. The one, *D. scheuringi,* has been mentioned before.

The other (Plate 31, Figs. 13-14) is a smaller form resembling *D. flexicaudum*. Elongate—0.300 mm. to 0.400 mm. long, width less than one-half the length. Small holdfast organ separated from acetabulum by a space. Occasionally contracted into a broad heart-shaped form. At other times it remains elongate but inverts its shoulder suckers. This worm is like *D. flexicaudum* in that it is found in the lens of its host, which frequently is so heavily infested that it appears opaque. The worms live in chambers in the interior of the lens—usually within its superficial layers. In an infested lens, examined under the microscope, the worms can be seen performing active contractile movements.

Diplostomulum sp. from *Lepibema chrysops*.—Diplostomulids (Plate 31, Fig. 12) probably from the humor; 0.312 mm. to 0.5 mm. in length, and a little more than half as wide. Broadly oval, the shoulder suckers bulging somewhat. Oral sucker large, prepharynx and esophagus short. Crura close together, pass posteriad in parallel fashion, diverge and sweep around the holdfast organ, pass dorsally over the excretory bladder, and terminate near the tail. Acetabulum close in front of holdfast organ, about the size of the oral sucker. Closely resembles our form from *Percina caprodes zebra* (compare the figures). In the diplostomulids from both of these hosts the crura are filled with an opaque substance. They are probably identical and possibly represent a new species of Diplostomulum.

Diplostomulum sp. from *Anguilla rostrata*.—Five specimens (Plate 31, Fig. 10) from the eye of the eel; 0.300 mm. in length and only slightly less broad than long. Heart-shaped with broad blunt anterior edge and more pointed posterior extremity. The cotylae project as two blunt muscular knobs. Esophagus and prepharynx greatly reduced. Acetabulum and oral sucker of approximately equal size. Probably a new species. At times the Diplostomulum secured from *Lota maculosa* agreed with *D. flexicaudum* in presenting a contraction phase somewhat similar to the worms here in question.

Diplostomulum sp. from *Schilbeodes miurus*.—About twenty specimens of this worm, from the lens of the host (Plate 31, Fig. 9). Shape and general anatomy similar to *D. flexicaudum*, also a lens inhabiting form. Length 0.315 mm.

Diplostomulum sp. from *Ameiurus natalis*.—Worms (Plate 31, Fig. 8) about 0.375 mm. in length. Found equally in lens and chambers of the eye. Also resemble *D. flexicaudum* to some extent, but differ from the preceding form in minor details. The holdfast gland is much more conspicuous, as is also the excretory bladder.

Biology of Diplostomulum

We find no evident limitation of Diplostomulum to any particular region of the lake. Infested fish are found at all depths and in all locations. The distribution is general. Infested perch were taken from such typical shoreline habitats as Big Bay, Shepherd's Point, Short Point Bay, and Lower South Bay; and from deep-water localities off Cleveland and Shackleton Shoals. The same applies to other hosts. Infested Lota with impaired lenses were taken in a trawl one mile off Cleveland in fifty-five feet of water. Suckers bearing what appears to be the same species (*Diplostomum flexicaudum*) were taken at the mouth of Black Creek in Cleveland Harbor. Practically all shoreline localities are represented in the infestations, as likewise most of the deep-water areas. Diplostomulum infestation is apparently independent of depth and bottom. The habits of the final hosts—usually gulls or terns—would fit in with such a distribution, since these birds are ubiquitous over the lake, alighting on the open water so that their egg-bearing excrement drops everywhere upon the bottom. The life history is unknown for some of the species, but evidently the primary, snail host must also be widely scattered, or possibly the parasites are adapted to a number of different snail hosts, just as the same species of Diplostomulum is apparently able to infest different species of fish. Cort and Brooks (1928:183) found several species and varieties of lymnaeid snails serving *Cercaria flexicauda* as host. The demonstration of the identity of this species of cercaria and Hughes' *Diplostomulum gigas* by Van Haitsma adds further evidence to explain the general distribution of this parasite in Oneida Lake, for Baker's earlier studies have given ample proof of the wide and general occurrence of lymnaeids in the lake. That both the deep and the shallow-water perch are evenly infested with the same species proves the general distribution of the infestive stages of this holostome on the bottom. For, in view of our other ecological findings in this paper, it would hardly seem true in general that fish acquire their parasites far from where they are caught.

The taking of perch in the middle of the winter, through the ice, with infested eyes, shows that the infestation persists through this season. Such heavily infested perch were taken in Big Bay, December 27, 1930, and in Lower South Bay, January 21, 1931.

Larval Genus Tetracotyle

Three species of this larval genus have been reported from fishes of the eastern United States. All the members of this group are thought to reach sexual maturity in the bodies of fish-eating birds. The adult worm is known for but one of these species. LaRue (1932) has made detailed studies of *Tetracotyle communis* Hughes and has shown that this metacercaria in herring gulls transforms to a sexually mature parasite recognized as belonging to the holostome genus Cotylurus. In consequence, *T. communis* assumes the name *Cotylurus communis*. The status of the remaining tetracotyles remains unknown. Hence in the present report it has seemed expedient to treat this group primarily from the point of view of host records.

In Oneida Lake a number of different fishes harbor tetracotyles, many of which are clearly normal infestations. Some are plainly pseudo-infestations, as those records of Tetracotyle from the stomach and intestine of *Micropterus salmoides, M. dolomieu,* and *Perca flavescens.* Tetracotyle larvae are not parasites of the digestive tract and cannot be considered as properly belonging in such a location. They have obviously been introduced here along with the original host which was taken in as food.

All of our Tetracotyle appear much alike in general anatomy. The genus may best be defined by quoting R. C. Hughes (1928): "The name Tetracotyle is here used in its restricted sense, namely, to include only those strigeid metacercariæ having lateral cotylæ, a slightly developed hindbody and a reserve bladder consisting of an irregular continuous coarse-meshed network of spaces, not in the form of definite vessels."

Very few species of Tetracotyle have been described from fish in this country. R. C. Hughes (1928) described *T. communis* from *Stizostedion canadense griseum*, *Percopsis omisco-maycus*, and *Catostomus commersonii*, of Douglas Lake, Mich. These worms were found in great abundance in the pericardial cavity. LaRue (1932) reports that Van Haitsma, after examining reared specimens originating from Percopsis hearts, concluded that they were identical with worms which were obtained from gulls after these had been fed hearts of suckers.

Hughes also described *Tetracotyle diminuta*. The type material was taken from 15 specimens of *Perca flavescens*, from Wampler Lake, Mich. He states, "In these fishes the parasites were found only on and about the heart, but they were not sought in other parts of the body. Similar parasites apparently conspecific with the type material were found in great numbers in *Perca flavescens* Mitchill and *Percopsis omisco-maycus* Walbaum from Douglas Lake, Michigan, during the summer of 1927. In these latter fishes the parasites were also sometimes found encysted in the walls of the eyes and in the adipose tissue of the eye sockets. In *Perca flavescens* all of the Tetracotyle were of this type, but in *Percopsis omisco-maycus* a larger form, probably *Tetracotyle communis*, was also found." The perch has never been found as a normal host to Tetracotyle in Oneida Lake.

Tetracotyle intermedia was described in the same paper by the same author. These worms are from the pericardium of the two whitefishes—*Prosopium quadrilaterale* and *Leucichthys artedi*—from Lake Huron, near St. Ignace, Mich. To our knowledge these three species are the only Tetracotyle described from fishes in this country.

The members of this genus show great individual variation in body size and in shape and relative size of the various organs. Some of the specimens from Oneida Lake fishes are readily identifiable. Others show variable characters or a combination of characters, deemed distinctive of two different species, in such confusion that the Tetracotyle group will be dealt with in this report wholly on the basis of host species.

Tetracotyle from *Catostomus commersonii*.—(Text Fig. 8, 3). From pericardium of host, attached to ventricle. Enclosed in outer soft, fatty cyst and inner membranous layer. Worms ovate, somewhat longer than broad. Specimens ranging from 0.495 mm. to 0.750 mm. in length. Oral sucker somewhat smaller than acetabulum. Pharynx small, crura terminate dorsal to holdfast organ. Resembles *Tetracotyle communis*. The size range of *T. communis* is given by Hughes as 0.51 mm. to 0.75 mm. in length. This is very closely coincident with the range observed in our worms. *C. commersonii*, the source of our material, was noted by Hughes as a host of *T. communis*, the pericardial cavity in both cases being the site of infestation. We therefore recognize this material as *Tetracotyle communis*. La Rue (1932) and Van Haitsma (1931) give proof of the identity of the worms from the sucker and some of those from Percopsis as set forth above. Herring gulls of Oneida Lake doubtless carry the adult, *Cotylurus communis*.

Tetracotyle from *Percopsis omisco-maycus*.—Numerous in this host (Text Fig. 8, 4). Our notes give the location as "mesenteries and heart," with the additional information, "like those on sucker hearts". A closely fitting inner cyst occurs, of tough membranous character, and this is surrounded by a larger, soft, fatty cyst. Size ranges from 0.675 mm. to 0.750 mm. in length. Oral sucker and acetabulum equal, the holdfast organ usually markedly larger than acetabulum. Pharynx small. The worm is within the size range of *T. communis,* near its upper limit. However, it differs from *T. communis* in the relative size of suckers and holdfast organ. In *T. communis* the suckers are as a rule unequal, and the holdfast organ and acetabulum approximately equal. In general, the worms from Percopsis have equal or subequal suckers, while the holdfast organ is much larger than the acetabulum. This condition is comparable to the proportions found in *T. diminuta,* reported by Hughes from Percopsis, but the large size of our worms rules them out of this species, which is given by Hughes as 0.155 mm. to 0.233 mm. in length for 10 mounted specimens.

These individuals from Percopsis showing perplexing confusion of characters may be a new species, with the proportions of *T. diminuta,* but the size of *T. communis.*

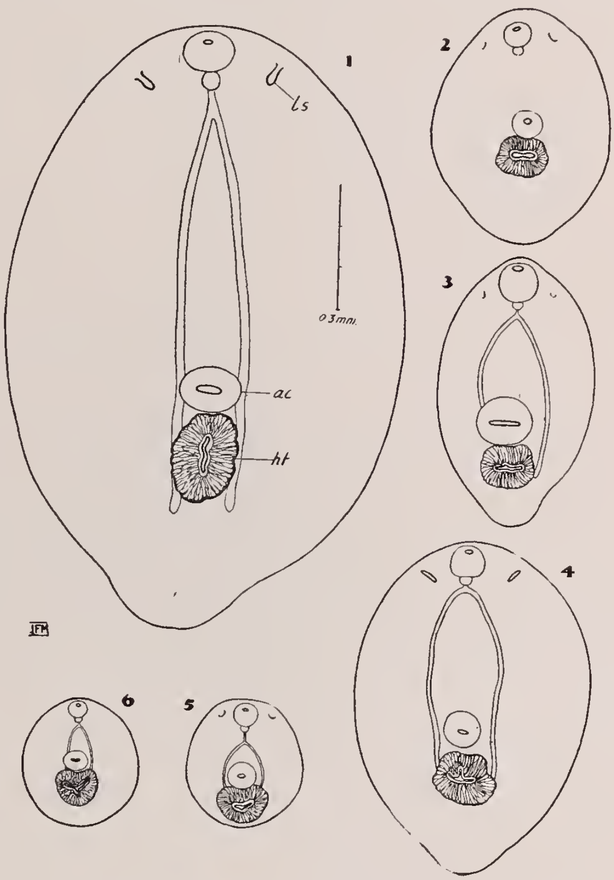


Fig. 8. Tetracotyle, various species drawn to same scale. 1, *Tetracotyle* sp. from *Percina c. zebra.* 2, *Tetracotyle* sp. from *N. crysoleucas.* 3, *Tetracotyle* sp. from *C. commersonnii.* 4, *Tetracotyle* sp. from Percopsis. 5, *Tetracotyle* sp. from *Leucichthys a. tullibee.* 6, *Tetracotyle* sp. from gut of *M. salmoides.*

ac—acetabulum, hf—holdfast organ, ls—lateral sucker.

Tetracotyle from tullibee.—A few worms (Text Fig. 8, 5) from the pericardium. Surrounded by a thick, tough, inner cyst and a larger, delicate outer cyst. The form is rounder than in the foregoing species, 0.300 mm. in length by 0.270 mm. in width. Acetabulum slightly larger than oral sucker; holdfast organ larger than acetabulum. Pharynx somewhat larger than in preceding species. The worm is easily recognized as *T. intermedia,* but is near the lower limit of the size range of this form. The type host is given by Hughes as *Prosopium quadrilaterale,* and *Leucichthys artedi* is recorded as host of apparently the same species. Both are whitefishes, which gives additional support to the determination of the Oneida Lake material from Leucichthys.

Tetracotyle from *Notemigonus crysoleucas.*—Abundant material of this form (Text Fig. 8, 2) from the viscera and mesenteries of the host. Cyst wall rather thin. Worms 0.255 mm. to 0.525 mm. in length, 0.150 mm. to 0.405 mm. in width. Suckers equal or subequal; holdfast organ large. Acetabulum in the middle or slightly anterior to middle of body. Pharynx small. Size variation great but continuous. This form cannot be regarded as *T. communis* because the average size is too small for this species and the proportions of the suckers and holdfast organ are different. In general, these worms are too small for *T. communis* and too large for *T. diminuta*. They come nearest to the size range and have the proportions characteristic of *T. intermedia*—with equal suckers and large holdfast organ. They differ from *T. intermedia* in that this species is reported from the pericardium of whitefishes, whereas the form in hand was found scattered throughout the body cavity of the shiner.

Tetracotyle from *Percina caprodes zebra*.—A few cysts (Text Fig. 8, 1) from mesenteries of the host. They are the largest members of the group in our collection, 0.945 mm. in length by 0.600 mm. in width. Oral sucker and acetabulum equal, holdfast organ larger than acetabulum. Cyst wall clear and closely applied, divided into an outer and an inner layer of approximately equal thickness. This worm is much larger than any previously described species. No Tetracotyle has hitherto been recorded from Percina, and in all probability this form represents a new species.

Tetracotyle sp. from *Micropterus salmoides*.—(Text Fig. 8, 6) Abundant in gut of a single specimen of large-mouth black bass from Short Point Bay. Ectopic, and must have been introduced along with food. Their proper host may have been some other small fish, which fell prey to the bass.

Worms surrounded by an inner cyst wall—a clear membrane of moderate thickness, closely applied. Average specimen 0.300 mm. in length by 0.270 mm. in width. Suckers equal or subequal, oral sucker somewhat withdrawn into the body in encysted specimens. Holdfast organ large, about twice the size of the acetabulum. Pharynx relatively large, almost half the diameter of the oral sucker. This form resembles our *T. intermedia* from the tullibee.

Biology of Tetracotyle: The hosts of Tetracotyle are nearly all fish of the open water. The only apparent exception in our records is the golden shiner, infested specimens of which were taken from Fairchild Bay and Cleveland Harbor. The infested suckers were taken in gill nets at various depths. Suckers frequent the off-shore shelf on the edge of deep water. The other hosts were all taken by gill nets at various locations in deep water. Our records are all for the summer season, June to September. Since we examined no fish of these species during the winter we do not know whether the infestation is carried through the colder weather. It should be noted that *T. diminuta*, recorded by Hughes from the heart of Perca as type host, is apparently wholly lacking from the perch in Oneida Lake.

Larval Group Neascus Hughes, 1927

The larval group Neascus is defined by Hughes, its author, as follows (1927:–259): "Strigeid metacercariæ with both fore- and hindbodies well developed and distinctly set apart by a constriction; no lateral sucking cups; forebody leaf-like; holdfast organ well developed; reserve bladder highly developed, the smaller branches of which are usually anastomoses; calcareous granules mostly free in the circumambient fluid; encysted."

All members of this group occur as encysted metacercariæ. Seven species have been recorded from fresh-water fishes of North America, but studies on some of these seem to indicate that not all of the described species are valid. Some species live in characteristically pigmented cysts of the integument while others occupy non-pigmented cysts within the internal organs of the host. In the Oneida Lake fauna, *Neascus vancleavei, N. grandis,* and *N. oneidensis* have been found in visceral cysts of fishes, but evidences indicate that *N. oneidensis* may be a synonym of *N. vancleavei.* In addition, certain Oneida Lake fishes are frequently found parasitized with a Neascus which forms the above mentioned pigmented skin cysts, similar to those found in the case of *Neascus amblopliti*s, and *N. bulboglossa.* We have not done sufficient work on these cysts to determine just how many species of Neascus are represented.

Neascus vancleavei (Agersborg, 1926)

Synonym: *Diplostomum vancleavei* Agersborg, 1926.

Hosts.—These are listed serially below, for the following reasons.

We have taken Neascus larvae very similar to *N. vancleavei* from a number of hosts, and have found it difficult to arrive at satisfactory conclusions as to the relationship of many of them. The general anatomy in all cases is similar, but very obvious differences in proportion are evident, and whether or not these can be regarded as diagnostic of different forms is hard to decide. Because of the problems presented by the material it is most convenient to discuss our collection of this group of worms by hosts. Without experimental evidence, which is lacking, there is no adequate ground on which to decide whether the forms listed below constitute several different species, or are but variations of a single species.

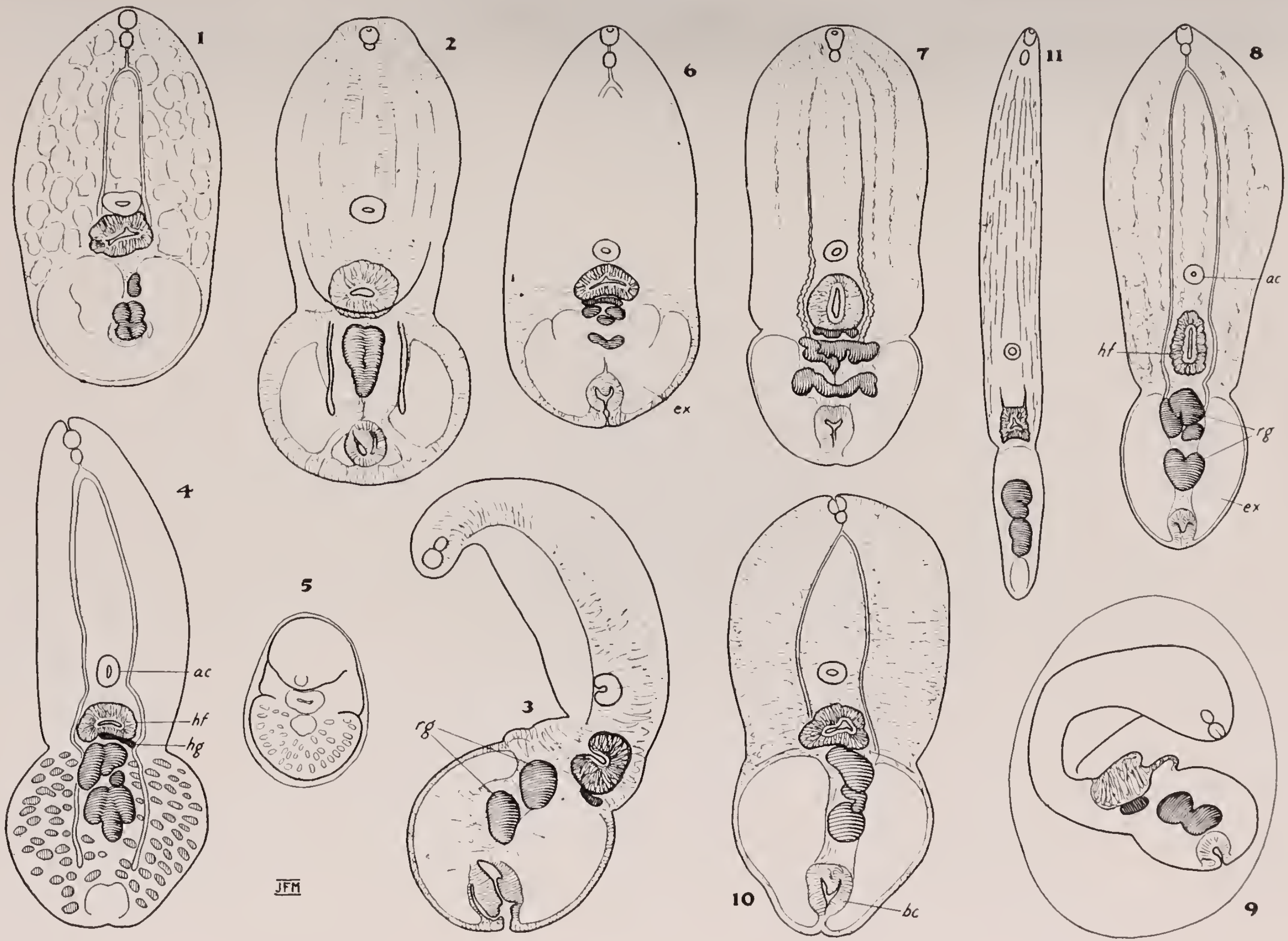
Neascus vancleavei from *Eupomotis gibbosus.*—Hughes reports this parasite from *Eupomotis gibbosus, Helioperca incisor, Ambloplites rupestris, Semotilus atromaculatus,* and *Hyborhynchus notatus.* He finds a minimum length for the species of 0.40 mm. and a maximum of 1.21 mm. The smallest worms were from *E. gibbosus,* the largest from *Helioperca incisor.* We have found *Neascus vancleavei* (Plate 32, Figs. 7–9) abundant in the sunfish, *E. gibbosus,* in Oneida Lake.

As in the case of our other holostome material these worms were dissected from their cysts, usually during life, preserved at once, and later stained and mounted for study. Mounted specimens, 0.450 mm. by 0.315 mm. to 1.5 mm. by 0.525 mm. Found in a thin-walled, large, loose-fitting cyst in which the worm is somewhat bent, and surrounded by an ample quantity of a granular fluid. The shape of our worms is very variable. Hughes' drawings show a type in which the anterior edge is blunt, with the oral sucker deeply retracted. The forebody is broadly ellipsoidal and the hindbody is equal in width to the forebody. In our specimens, however, such a condition does not prevail generally. Our worms more usually have a pointed anterior end, with oral sucker at the apex, and the broadest part of the forebody anterior to the middle. The hindbody is usually

Plate 32. *Neascus vancleavei* (?) from various hosts. (Drawn freehand, dimensions in text.) 1, From *Boleosoma n. olmstedi*. 2, 3, From *Fundulus d. menona*. 4, 5, From *Hybognathus regius*. 6, From *Percina c. zebra*. 7, 8, 9, From *Eupomotis gibbosus*. 10, From *A. rupestris*. 11, From *M. salmoides*.

ac—acetabulum, bc—bursa copulatrix, ex—excretory organ, hf—holdfast organ, hg—holdfast gland, rg—rudiments of gonads.

Plate 32



elongate acorn-shaped and much narrower than the forebody. This form seems typical of the most advanced larva. Oral sucker followed closely by the small pharynx, and a short esophagus is present. Acetabulum in posterior region of forebody, separated by a short distance from holdfast organ. Holdfast gland so closely applied to the dorso-caudal face of the holdfast organ that it is almost obscured by this structure.

Neascus vancleavei (?) from *Percina caprodes zebra.* (Plate 32, Fig. 6) Largest worms 0.705 mm. long by 0.330 mm. wide, smallest 0.450 mm. by 0.210 mm. Acetabulum close to holdfast organ. Excretory bladder large and filled with a gummy content. Hindbody poorly set off from forebody. Gonads appear small. These are probably young larvae which have not yet developed the typical features of Neascus. The cyst here is large and the worm lies within at full length.

Neascus vancleavei from *Fundulus diaphanus menona.*—(Plate 32, Figs. 2-3) Measurements 0.720 mm. by 0.330 mm. Hindbody spherical, large, with very thick walls. Excretory bladder small in proportion. Parenchyma of forebody thrown into longitudinal columns between vessels of excretory bladder. Anatomy otherwise typical of *N. vancleavei.*

Neascus vancleavei from *Hybognathus regius.*—Neascus has been collected from this host both from Oneida Lake, and from the Jamesville Reservoir. The worms (Plate 32, Figs. 4-5) from both localities are similar, and in some respects form a distinctive type. Average length 0.800 mm., width 0.300 mm. The worm fits snugly in the cyst and has the forebody somewhat bent. Proportions and general anatomy typical of *N. vancleavei,* but usually the excretory bladder in the hindbody contains an opaque substance arranged in a network of transverse bands—so that the hindbody appears filled with a dark reticulum. In other individuals this area appears clear as in typical worms. We have observed this condition of the excretory bladder only in Neascus from *H. regius,* and nowhere else. It is possibly a reaction to this host.

Neascus vancleavei from *Notemigonus crysoleucas.*—From the gut of the host, which cannot be regarded as their proper location. Introduced with food. Small, 0.600 mm. by 0.225 mm., and contained in a rather large cyst filled with a caseous material. What features can be discerned classify them as *N. vancleavei.*

Neascus vancleavei from *Micropterus salmoides.*—(Plate 32, Fig. 11) Ectopic, in the gut of the bass. No doubt introduced with food. They are very long and thin, about 1.125 mm. by 0.165 mm. Aside from this they are typical.

Neascus vancleavei from *Esox lucius* and *Perca flavescens.*—Ectopic, from gut of these fishes, described by us in the first part of this work as *Neascus oneidensis.* It seems probable to us at the time of this writing that they are specimens of *Neascus vancleavei.* Their shape is similar to other material of this species in our collections, but no pharynx is visible. However, this organ is frequently difficult to detect in known specimens of *N. vancleavei.*

Neascus vancleavei is apparently most abundant in shallow water. Most of our records are from such localities as Fairchild Bay, Fish Creek sloughs, Bridgeport, Brewerton, etc. However, infested *Boleosoma nigrum olmstedi* and *Percina caprodes zebra* have been taken in a trawl off Jewell, about half a mile from shore, in 30 feet of water. All of our records for Neascus are for the summer months. We know nothing about the infestation during the winter.

Neascus grandis Mueller and Van Cleave, 1932

Host.—*Umbra limi;* metacercariæ in cysts on the mesenteries.

Described in Part II of this report. No new collections have been made. The species seems to be specific for the mud minnow.

Neascus amblopitis Hughes, 1927

Synonym: *Neascus wardi* Hunter

Hosts.—*Esox niger, Esox lucius, Perca flavescens, Ambloplites rupestris, Eupomotis gibbosus* and others; metacercariæ in pigmented integumentary cysts.

This parasite was frequently encountered in Oneida Lake fish. It appears as an integumentary cyst, deeply pigmented and forming a slight surface elevation. Fish are at times found literally peppered with these parasites, and feel rough to the touch as a result of the numerous granular elevations. The cyst is surrounded by a very tough wall of fibrous connective tissue, and the worms can be dissected out only with great difficulty.

We did not study these parasites in any detail. Some of the cysts were dissected, and the metacercariæ which emerged seemed to be *Neascus amblopitis.* However, it is probable that other species are also present in Oneida Lake, such as *Neascus bulboglossa,* which also occurs in integumentary cysts, similar to those of *N. amblopitis.*

The parasitized fishes are found in shallow water. Apparently deep water fishes were either free of the infestation, or at most had it only very lightly. The worst infestations are usually found on perch and pickerel (*E. niger*) taken in small, shallow, protected bays and coves where the bottom is muddy.

General Conclusions on Larval Holostomes

In Oneida Lake the group Tetracotyle is preferential in its host relationship to soft fishes, such as the whitefishes and suckers, or small fish and minnows, such as Percopsis or the golden shiner. Hughes, 1928, reported *T. communis* from *Stizostedion griseum,* and *T. diminuta* from *Perca flavescens,* the former from Lake Erie, and the latter from Wampler Lake, Mich. But in Oneida Lake the hard bodied fishes do not appear to be infested with Tetracotyle.

The different species of Neascus show different host adaptabilities. So far as we know *N. grandis* occurs only in the mud minnow. *N. vancleavei,* on the other hand, occurs chiefly in the smaller members of the sunfish family, but also in other smaller fishes, such as Boleosoma, Percina, Fundulus, and Hybognathus. It never occurs in the perch or pike perch. Metacercariæ of the *N. amblopitis* type, on the other hand, are scattered over a number of hosts, but seem to prefer perch and pickerel,—species which are not infested with *N. vancleavei.* Silurids are apparently not infested with either of the above large groups, either Neascus or Tetracotyle. Diplostomulum, however, in its various species, is the least discriminating of the three genera in its choice of host. It may occur, apparently, in almost any species of fish host.

Of the larval genus Diplostomulum as represented in Oneida Lake, there seem to be two major groups corresponding to the species *Diplostomulum* (*Diplostomum*) *huronense,* and *Diplostomulum* (*Diplostomum*) *flexicaudum.* Perch and trout-perch are heavily infested by the former. The latter is found in *Catostomus commersonii,* and also, we believe, in *Lota maculosa.* Milder infestations, however, occur in a great number of hosts, and in such cases we are unable to say for certain whether these are caused by one of the above species or a different form. However, we find Diplostomulum infesting two species of catfishes, various sunfishes, the brown trout, and various others. The lack of host specificity in the genus Diplostomulum has particular significance in the light of observations by Van Haitsma (1931a). This author finds that the cercariæ of Diplostomulum in penetrating the tissue of fishes frequently cause the death of the fish and are doubtless responsible for the death of many species in territory occupied by these larvae.

Family Azygiidae

The family Azygiidae comprises a few genera of trematodes which reach sexual maturity in fishes. Two of the included genera, Azygia and Leuceruthrus, are distinctive parasites of the stomach of fresh-water fishes. Of these, the latter has never been found in any of the hosts of the Oneida Lake fauna, while the former is rather abundantly represented in a diversified list of chiefly carnivorous fishes.

A voluminous literature treats of this family in North America. Historically, this is well treated by Manter (1926) whose publication dealt with both the marine and fresh-water representatives of the family. Since in the present study the genus Azygia alone is considered, no attempt will be made to treat the family as a whole.

Genus Azygia Looss, 1899

Generic Diagnosis.—Powerful, muscular distomes of elongate, slender proportions, and of pale reddish color in life. Body without spines, thick, and of approximately equal diameter throughout. Suckers well developed and powerful, oral sucker slightly larger than acetabulum, the latter near or anterior to the middle of the body. Prepharynx lacking, pharynx strongly developed, esophagus very short or wanting. Intestinal crura extend into the caudal tip. Vitellaria follicular, post-acetabular, lateral bands in all North American forms extending posterior to the testes. Gonads in posterior region, with ovary anterior to testes. Genital pore median, anterior to acetabulum. A spacious genital sinus receives the ducts of both sexes, of which the male duct consists of a ductus ejaculatorius, a prostatic part, and seminal vesicle. Uterus with many transverse folds between ovary and metraterm. Intrauterine eggs numerous. Excretory bladder tubular or sac-like, posterior to testes in caudal tip of body. The miracidium is not ciliated.

This genus inhabits the stomach of various fishes. During life the color of these parasites is reddish, doubtless from haemoglobin dissolved in their body fluid. They are among the most muscular of the flatworms of fishes. Because of their extreme muscularity, there is little regularity in shape and appearance of different worms of the same species even when fixed by the same method. Coupled with this circumstance is also the fact that the genus seems naturally variable in certain fundamental characters, such as the anterior and posterior limits of the vitellaria and the position of the gonads.

Due largely, if not entirely, to the foregoing factors, the genus Azygia has given unusual difficulties to workers in the past.

In the literature there are descriptions of seven species which have been considered by their respective authors as distinctive of the North American fauna. In addition, one European species has been recorded by some of the earlier workers on this continent. Thus eight specific names have been applied to the Azygia of North America, and there have been unsuccessful attempts to recognize three of these as representing other genera (Mimodistomum, Megadistomum, and Hassallius). By gradual steps it has been demonstrated that Azygia is highly inconstant in its morphological characters. Ultimately, in the monograph by Manter (1926), the list of species considered as valid for the North American fauna was reduced to three (*A. longa, A. acuminata,* and *A. angusticauda.*) In the opinion of the present writers, this list should be still further reduced by considering *A. acuminata* as a synonym of *A. longa.*

In the present study, approximately 150 specimens of Azygia have been collected from thirteen host species. Practically all of these specimens have been stained and prepared as permanent mounts on slides. Variation in this series of mounts is confusing, but continuous around two centers.

We have found no specimens of Leuceruthrus. This genus, closely allied to Azygia, is very obviously wanting in the Oneida Lake fauna.

Azygia longa (Leidy, 1851)

Text Figure 9, 6–7

Synonyms: *Distomum longum* Leidy, 1851; *Megadistomum longum* (Leidy) of Stafford, 1904; *Distomum tereticolle* of Leidy, 1851; *Azygia tereticolle* of Stafford, 1904; *A. sebago* Ward, 1910; *A. bulbosa* Goldberger, 1911; *A. acuminata* Goldberger, 1911; *Hassallius hassalli* Goldberger, 1911; *A. lucii* of Cooper, 1915.

Hosts.—*Anguilla rostrata, Amia calva* (Cross Lake), *Salmo fario, Percina caprodes zebra, Lota maculosa* ?, and *Boleosoma nigrum olmstedi* ?; in stomach.

This species is distinguished by its great length and by internal topography. Vitellaria begin posterior to acetabulum and stop well short of posterior tip of body. Gonads a quarter of the body length, more or less, from the posterior end. Varies in appearance when taken from different hosts. The host relations, as revealed by published records of occurrence, are perplexing. Anguilla, Amia, and Lota are the only hosts for *Azygia longa* in Oneida Lake, which coincide with host records for this species, or its synonyms, by other writers. *Salmo fario, Percina caprodes zebra,* and *Boleosoma nigrum olmstedi* are hosts here recorded for the first time. Perca, Stizostedion, and *Esox niger,* are recorded by other workers as hosts for species definitely proved as synonymous with *Azygia longa,* but have not been found to harbor this parasite in Oneida Lake. Obviously the species has a wide range of host tolerance. In Oneida Lake, the eel is the most important host of *A. longa.*

Specimens of *A. longa* from Amia of Cross Lake are much more slender than those from the eel. The largest specimens from the eel are about 28 mm. long, while those from the bowfin are about 19 mm. From the brown trout we have taken worms which agree in general topography with those from typical hosts, but are diminutive forms not more than 5 mm. long.

In all of these worms, from various hosts, there is a considerable distance between the gonads and the caudal tip—usually one-fifth to one-fourth of the body length. In the worms from the eel the gonads are located the greatest distance from the caudal tip. In some of these specimens, fully a third the length of the body lies posterior to the second testis. In the specimens from Amia this distance is less. In those from the brown trout the proportion of this distance to the length of body is about the same as in the specimens from Amia; in most cases—about one-quarter the length of the body, but in a few cases it is reduced—the gonads lying nearer to the tail, forming a transition to the condition found in *A. angusticauda*. The frequent occurrence of intermediate forms suggests that possibly these species may intergrade and later be proved identical, but we are inclined, on the basis of evidence in hand, to regard the species as separate.

We also have a few doubtful specimens of *A. longa* from *Percina caprodes zebra,* and a few from Boleosoma, and Lota, too young to identify definitely. They were intermediate in their characters and might be either this species or *A. angusticauda.*

Manter made careful comparative studies, mostly on the original material, and his table of synonyms for *A. longa* is without doubt correct as far as it goes. After a review of the literature we not only accept Manter's conclusions, but feel that he has not been sufficiently inclusive in his synonymy. Reviewing Goldberger's work (1911) we conclude that *A. acuminata* and *A. bulbosa* are synonyms. They are both from the stomach of Amia, and agree in the asymmetrical wavy character of the crura, and the location of the gonads. Since, according to Manter, *A. bulbosa* is a synonym of *A. longa, A. acuminata* should also become a synonym of this species. The characters given in Manter's key for separation of *A. acuminata* and *A. longa,* are unreliable for differentiating species in the genus Azygia. Width or length, or contraction of the neck, are of little significance in such muscular worms. Location of the anterior vitelline follicles is an important character in this genus. There is no significant difference in egg sizes. The only remaining difference lies in the character of the internal (parenchymal) muscles. This character is a very dubious one. Altogether there seems no justification for maintaining *A. acuminata* as a distinct species. We regard it as *A. longa* from the stomach of Amia, a recognized habitat for *longa,* and accordingly have added *A. acuminata* to the already long list of synonyms.

The important host of this worm in Oneida Lake is the eel, in the stomach of a single individual of which as many as eight or ten of these worms may be found. The instance of the occurrence of *A. longa* in *Amia calva* from Cross Lake, New York, is recorded here, for although Amia has not been taken by us in Oneida Lake, it is known to occur in the Oneida River. The other hosts listed for *A. longa* are evidently incidental and unimportant. None of the trout from the Cleveland mill pond or Black Creek were infested with Azygia, but three of the six brown trout taken in the lake were infested. One of these (a fifteen-inch fish) had six worms in its stomach; another (sixteen inches) had two; the third (eighteen and one-half inches), one. The other three fishes, 15, 15 and 19 inches in length, were all negative for Azygia. These figures indicate a fifty per cent incidence of *A. longa* in the brown trout in the lake, and absence of the parasite in the trout from the streams.

Azygia angusticauda (Stafford, 1904)

Text Figure 9, Figures 1–5

Synonyms: *Mimodistomum angusticaudum* Stafford, 1904; *Azygia loossii* Marshall and Gilbert, 1905.

Hosts.—*Perca flavescens, Micropterus salmoides, M. dolomieu, Ambloplites rupestris, Esox niger, Eupomotis gibbosus, Stizostedion vitreum* (?), *Lota maculosa* (?), *Boleosoma nigrum olmstedi* (?). In stomach.

This species is usually under 5 mm. in length, with characters in general similar to *A. longa*. However, the acetabulum is relatively farther back even in fully grown specimens. Vitellaria from close behind the acetabulum to the tail end of the body in most specimens. In some they stop somewhat short of this limit. Gonads very near the caudal tip, occasionally removed from it by a space equal to about one-sixth of the worm at most, but this condition is uncommon and probably attributable to the dilation of the excretory bladder. Crura pass to posterior end, straight and parallel, except where excessive longitudinal contraction causes them to be more or less wavy. Pharynx immediately behind oral sucker, esophagus lacking. Uterus from the gonads to the acetabulum.

In Oneida Lake the perch and large-mouth black bass are the chief hosts. There are records of single instances of occurrence in the following additional hosts: *Micropterus dolomieu, Esox niger, Eupomotis gibbosus, Ambloplites rupestris;* and somewhat doubtful determinations of immature individuals from *Boleosoma nigrum olmstedi, Lota maculosa,* and *Stizostedion vitreum.* Investigators in other localities have reported *A. angusticauda,* or one of its synonyms, from Lota and from Stizostedion. Neither the perch nor *Esox niger* has been previously recorded as a host for this species, though the perch seems one of the most characteristic hosts in the Oneida Lake fauna.

One specimen (Text Fig. 9, 2) from the stomach of *Stizostedion vitreum* has been identified as *A. angusticauda,* though its individual peculiarities offered numerous difficulties. The host was secured from Davidson's Fish Market in Brewerton and was said to have come from Oneida Lake. The single specimen of Azygia found in this pike perch is markedly different from other individuals of the species. In its length (20 mm.) the parasite far surpasses the 5 mm. characteristic of other specimens. The specimen was flattened preparatory to killing and in this condition has a transverse dimension of almost 4 mm. The length would suggest a determination as *A. longa,* but the location of the gonads at the extreme caudal tip eliminates this species from consideration.

A careful search of the collections has failed to reveal other forms of Azygia similar to this single specimen from the pike perch. One other specimen from the same host (Text Fig. 9, 3) is 7.5 mm. long and therefore larger than typical *A. angusticauda*, but only a little more than a third the size of the unique specimen just discussed.

Several Azygia from the perch are similar in character of the crura to the large specimen from Stizostedion. These worms are about 1.3 mm. wide and 5 mm. long. The crura anterior to the acetabulum are thrown into symmetrical waves. The gonads are near the posterior tip. In general the anatomy is that of *A. angusticauda*. (Text Fig. 9, 1).

In spite of the fact that the perch has not been recorded previously as a host for *A. angusticauda*, in Oneida Lake the two principal hosts of this parasite are the yellow perch and the large-mouth black bass. The worms from the perch look a little more flourishing than those from the bass, and apparently the perch is the more favorable host. We have records of the parasite from about forty perch. These are all from shallow shore waters, the following localities being represented: Old Man Bay, Dunham Island, west shore of Walnut Point, Shepherd's Point, Johnson's Bay, Poddygut Bar, Short Point Bay, Lower South Bay, Big Bay. We do not have a single record of infestation with Azygia for deep-water perch. The average infested perch carries two or three worms in the stomach. Both species of Azygia are very constant in their selection of the stomach as a habitat. Under normal conditions the worms are never found in other portions of the alimentary tract.

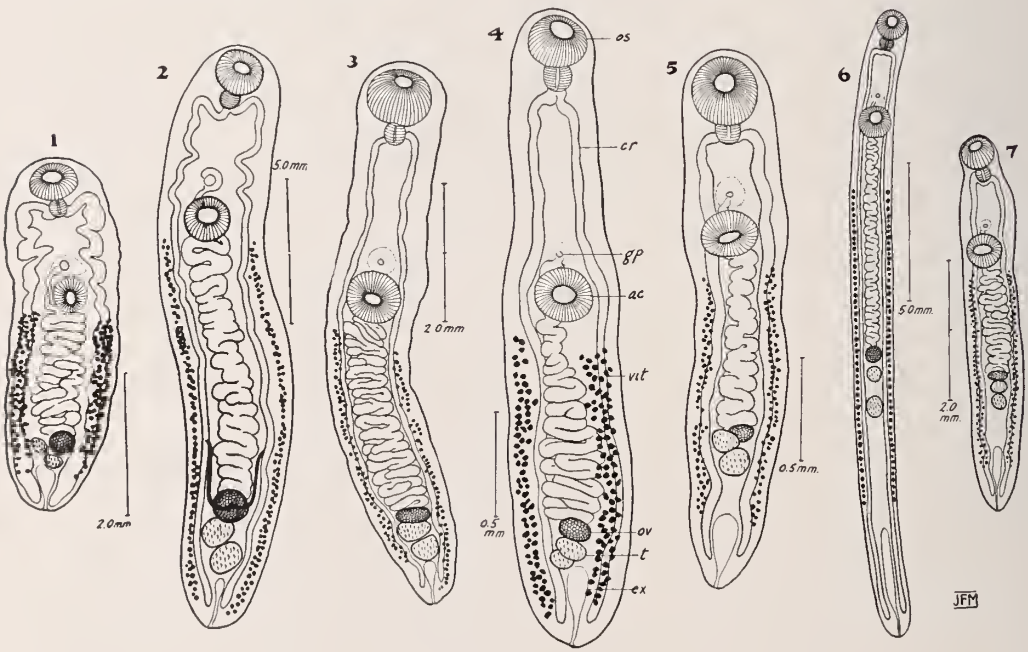


Fig. 9. Azygia.

Azygia angusticauda. 1, from perch. 2, very large worm from Stizostedion. 3, from Stizostedion. 4, from perch. 5, from *M. salmoides.*

Azygia longa. 6, from eel. 7, small worm from brown trout.

ac—acetabulum, cr—crura, ex—excretory bladder, gp—genital pore, os—oral sucker, ov—ovary, t—testes, vit—vitellaria.

Azygia angusticauda from the large-mouth black bass show their ecological affinities with the above, in that the large-mouth bass is exclusively a shallow- or shore-water fish. Large-mouth black bass infested with *angusticauda* have been taken in the following localities: Big Bay, Fairchild Bay, west shore Walnut Point, Short Point Bay, Old Man Bay and Lakeport Bay. It is of interest to note that in the deep-water *M. dolomieu* only a single specimen of this worm has been found. In contrast, about forty per cent of the large-mouth black bass are infested with this parasite. The numbers found in a single fish are small, as in the case of the perch, not more than three or four, as a rule. The records from *Boleosoma nigrum olmstedi, Lota maculosa, Ambloplites rupestris, Esox niger* and *Eupomotis gibbosus* are based on a single infestation in each case.

There is an ecological contrast between the two species of Azygia. *A. angusticauda* is found only in fish taken from shore situations and evidently belongs in the shallow water. Its normal hosts are the shallow-water yellow perch and the large-mouth black bass. On the other hand, *A. longa* has as its normal host in Oneida Lake, the eel, a deep-water fish, and apparently belongs in the deep water. A number of Azygia were secured from perch during the winter—Dec. 27, 1930, and Feb. 28, 1931, at Big Bay and Lower South Bay. The rest of our records are for the summer months. Evidently there is no seasonal restriction to infestation in this group.

SECTION 3. TAXONOMY AND BIOLOGY OF THE CESTODA OF ONEIDA LAKE FISHES.

The Cestoda or tapeworms are less numerous than the trematodes in the fishes of Oneida Lake, with respect both to numbers of individuals and to number of species represented. In their adult state cestodes never occur outside the digestive tract of the fish. The habitat relation is thus much more restricted than for the trematodes. On the other hand, there is much greater flexibility in the number of and host relations of the stages during ontogeny. While most of the trematodes have a reproductive cycle in the body of the larval host, one cestode egg ordinarily gives rise to but one tapeworm. The larval tapeworm usually develops within the body of an arthropod and may become immediately established in the digestive tract of the fish which devours the arthropod. Among many fish tapeworms, additional hosts may be intercalated, either serving solely as shelter for the individual parasite, or representing an essential link in the chain of host relationships. In addition to their serving as host for adult tapeworms, fishes very commonly shelter advanced larvae of worms which reach sexual maturity in other fishes, in birds, or even in mammals.

The mature tapeworm consists of a terminal organ of attachment known as the scolex, and a body containing one or many sets of reproductive organs. In the most characteristic tapeworms the body is divided into many segments or proglottids, each of which contains an entire set of male and female reproductive organs. Some tapeworms lack this division into proglottids, while certain of the most primitive forms have but a single complement of reproductive organs. Consequently the most primitive cestodes resemble the trematodes, from which, however, they are readily distinguishable in that they have no trace of digestive organs.

In the older systems of classification, all of the cestodes bearing a single set of reproductive organs were lumped into a group known as the Cestodaria. Some of these worms in details of structure so closely resemble some of the chain-forming tapeworms that recent investigators have avoided the assumption that simplicity in number of bodily units indicates a single natural group. Thus Poche (1926) recognizes two subclasses of the class Cestoidea. The first of these, the Amphilinoinei, include the primitively simple cestodes, while the Taenioinei comprise all of the tapeworms bearing many proglottids, as well as a few of their close relatives which lack chain formation. None of the Amphilinoinei occur in the Oneida Lake fauna, hence all of the tapeworms considered in this report belong to the subclass Taenioinei. In grouping the genera and families of this subclass, Poche (1926) has recognized four orders, all but one of which find representation in the Oneida Lake fishes.

Cestoda: Order Bothriocephalidea

This order has gone under the name Pseudophyllidea in the works of many authors. Most of its members are characterized by the possession of two simple sucking grooves on a scolex which lacks a rostellum and proboscis-like organs. As represented in the Oneida Lake fauna, this order includes seven genera, which may be separated by the use of the following key.

Key to the Genera of Bothriocephalidea From Oneida Lake Fishes

1 (a) Body consisting of a scolex and but one set of reproductive organs **Family Caryophyllaeidae** 2
  (b) Body consisting of a scolex followed by numerous sets of reproductive organs..... 4
2 (a) No vitelline follicles posterior to ovary........ **Monobothrium**
  (b) A group of vitelline follicles posterior to ovary........ 3
3 (a) Scolex with three pairs of loculi or bothria........ **Glaridacris**
  (b) Scolex with one pair of well defined acetabulum-like suckers, with or without additional loculi........ **Biacetabulum**
4 (a) Scolex bearing four chitinized plates with three recurved hooks borne on each........ **Triaenophorus**
  (b) Scolex without hooks........ 5
5 (a) Strobila not divided into proglottids. In body cavity of fishes........ **Ligula**
  (b) Strobila divided into proglottids. In digestive tract of fishes........ 6
6 (a) Cirrus and vagina opening at margin of proglottids........ **Abothrium**
  (b) Openings of cirrus and vagina near middle of dorsal surface of proglottids........ **Bothriocephalus**

Family Caryophyllaeidae

Hunter (1927, 1929, 1930) has recognized fifteen genera under the family Caryophyllaeidae. Of these the genera Monobothrium, Glaridacris, and Biacetabulum have been found in the Oneida Lake fauna. The reader should refer to Hunter's publications for an extended consideration of this family. The following diagnosis is condensed from Hunter, 1930.

Genus Monobothrium Diesing, 1853

Generic diagnosis: Caryophyllaeinae with scolex round to oval in cross section, bearing 6 shallow longitudinal grooves and terminal funnel-shaped introvert. Ovary H-shaped, uterine coils never anterior to cirrus sac. Post-ovarian vitellaria may or may not be present. Parasitic in digestive tract of Cyprinidae and Catostomidae. Development unknown.

This genus contains two species, *M. wageneri* Nybelin, 1922, and *M. ingens* Hunter, 1927. The former is a European species and probably does not occur on this continent.

Monobothrium ingens Hunter, 1927

Plate 33, Figure 3

Host.—*Catostomus commersonnii,* in intestine.

First taken by Hunter from *Ictiobus cyprinella* and not listed as occurring in any other host. Our specimens from *C. commersonnii* represent a new host for the species. The following description is abbreviated from Hunter (1930:38)

Specific Diagnosis: Adult parasites embedded in pits in mucosa of intestine. Length 45 mm. to 75 mm.; width 0.9 mm. to 1.2 mm. Neck distinct, 4 mm. to 5 mm. long, 0.69 mm. maximum width. Longest longitudinal grooves on dorsal and ventral surfaces. Body broadens posteriorly, oval in cross section. Testes 300 to 325, roughly ellipsoidal. Wings of ovary 0.8 mm. to 1 mm. long. Post-ovarian vitellaria absent. Eggs 0.053 mm. to 0.058 mm. by 0.028 mm. to 0.033 mm.

We have several specimens of this worm in our collections. They are readily distinguishable from the remaining cestodarian material on the basis of their large size, character of the scolex and lack of post-ovarian vitellaria. The suckers harboring these came from the mill pond at Cleveland.

Genus Glaridacris Cooper, 1920

The genus Glaridacris was established in 1920 to receive a species which Cooper found in the digestive tract of suckers living in Douglas Lake, Michigan. Prior to that date there had been incidental mention of the occurrence of cestodarians in the fresh-water fishes of this continent, but the works of Linton (1893 and 1897) were the only ones in which specific determination of the worms was attempted. Subsequently, there have been intensive studies, especially by Hunter (1927, 1929, 1930), who recognizes four species of Glaridacris from fresh-water fishes. Two of these species have been found in Oneida Lake. Thirty-four suckers were examined, from the Oneida Lake area of which 11 bore cestodarian infestation. The genus Glaridacris occurred in 10 of these, the number per fish varying from one to 5 or 6. In one instance only were the worms found with the scolex buried in a crater-like depression of the intestinal wall, as described by Cooper (1920:6). The following diagnoses of the genus and species are modified from Hunter (1930).

Generic diagnosis: Caryophyllaeinae with three pairs of loculi or bothria on well defined scolex, which may or may not form a definite terminal disc. Cirrus opens on ventral surface or into a shallow, non-eversible genital atrium. Ovary H-shaped; coils of the uterus never extend anteriorly to cirrus sac. Terminal excretory bladder and external seminal vesicle present. Post-ovarian vitellaria present. Parasitic in digestive tract of the Catostomidae.

Glaridacris catostomi Cooper, 1920

Plate 33, Figure 1

Host.—*Catostomus commersonnii.* In intestine.

Specific diagnosis:—Adults up to 25 mm. in length with a maximum breadth of 1 mm.; may be buried in pits in mucosa, although this condition is more typical of the larvae. Scolex short, broad and chisel-shaped, length varying between 0.3 mm. and 0.45 mm. Neck distinct, slightly narrower than body, which is flattened dorso-ventrally, and bears a conspicuous genital atrium. Testes number between 405 and 420. Vagina median, ventral, convoluted, and forms an indistinct receptaculum seminis. Wings of ovary compact and rounded, 0.65 mm. to 0.9 mm. long. Egg operculate, 0.054 mm. to 0.066 mm. by 0.038 mm. to 0.048 mm.

We have 22 individuals of this worm in our collections, from 6 fish taken from the mill pond at Cleveland.

Glaridacris confusus Hunter, 1929

Plate 33, Figure 2

Host.—*Catostomus commersonnii,* in intestine.

Specific diagnosis: Adults usually 3 mm. to 7 mm. by 0.2 mm. to 0.8 mm. flattened dorso-ventrally. Scolex oval at base, tapering to a chisel-shaped extremity which is cut by 6 loculi. Testes large, 0.1 mm. to 0.3 mm. by 0.1 mm. to 0.13 mm., numbering 25 to 35, in two parallel rows. Male and female reproductive organs open on surface, 0.020 mm. to 0.055 mm. apart. Ovary H-shaped, with lateral wings very long and narrow. A small cluster, of 5 or 6 vitelline follicles between posterior tips of ovary. Eggs small, ovoid, 0.037 mm. to 0.048 mm. by 0.020 mm. to 0.031 mm.

We have numerous worms of this species from *C. commersonnii.* Two of these suckers were from the mill pond at Cleveland, and several specimens from the lake near Cleveland. Our specimens are somewhat larger than Hunter's figures indicate. Some of our worms are 10 mm. in length, whereas Hunter gives 7 mm. as the maximum length.

The two species *G. catostomi* and *G. confusus* are readily distinguished by the shape of the ovary and the cluster of post-ovarian vitellaria. These latter are few in *G. confusus,* but numerous and form a V-shaped cluster in *G. catostomi.* In *G. confusus* the vitellaria are limted to the lateral fields, whereas in *G. catostomi* they are scattered throughout the median field. There are further differences in that the neck of *G. confusus* is broad and short, and at their anterior limits testes and vitellaria begin at the same transverse level. In *G. catostomi,* on the other hand the neck is long and slender, and the vitellaria precede the testes, invading the median field in a long wedge-shaped arrangement.

Hunter reports *G. confusus* from the following hosts: *Ictiobus* sp., *Ictiobus bubalus, Dorosoma cepedianum. Catostomus commersonnii,* the source of our material, represents a hitherto unrecorded host of the species.

PLATE 33

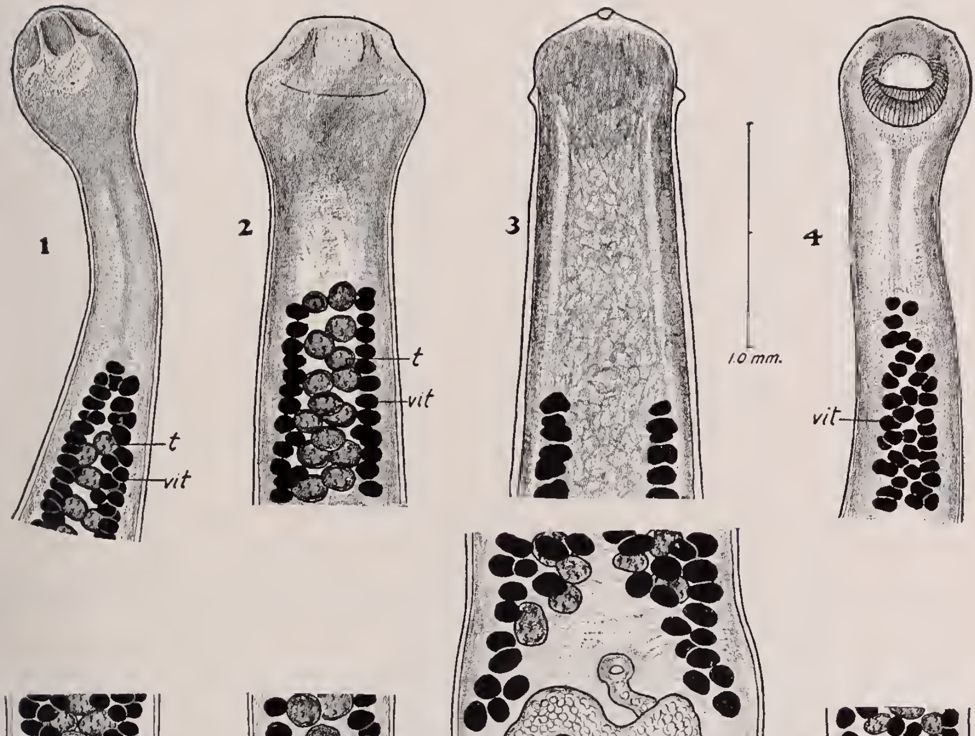


Plate 33. Cestodaria. (Showing head and tail only, of each species. Drawn to scale shown with 4.) 1, *Glaridacris catostomi.* 2, *Glaridacris confusus.* 3, *Monobothrium ingens.* 4, *Biacetabulum infrequens.*

ov—ovary, pv—post-ovarian vitellaria, t—testes, ut—uterus, vit—vitellaria.

Genus Biacetabulum Hunter, 1927

This genus was established by Hunter to include three species, all from American fishes. We have what appears to be material of one of these species, *B. infrequens,* from the common sucker in Oneida Lake. The following descriptions are condensed from Hunter (1930).

Generic diagnosis: Caryophyllaeinae with a well defined scolex, varying but little in shape, bearing one pair of well defined acetabular suckers, with or without additional loculi. Cirrus opens into the utero-vaginal canal before it reaches the surficial atrium. Ovary H-shaped; uterine coils extend anteriorly to cirrus sac, reaching a maximum longitudinal extent of one-fourth that of the testicular field, usually less. Post-ovarian vitellaria present. Parasitic in the Catostomidæ. Development unknown.

Biacetabulum infrequens Hunter, 1927

Plate 33, Figure 4

Host.—*Catostomus commersonnii,* in intestine.

Specific diagnosis: Adults from 16 mm. to 22 mm. in length by about 0.6 mm. in breadth. Acetabular suckers 0.168 mm. to 0.24 mm. in diameter. Neck distinct, having a maximum length of 0.5 mm. Body oval in cross section. Testes number between 420 and 440. Wings of ovary 0.608 mm. to 0.658 mm. long. Vitellaria surround the testes.

This species differs from *B. giganteum* chiefly in the character of the scolex which in this latter form bears two pairs of loculi in addition to the two acetabular suckers. *B. giganteum* is also recorded as 7 mm. to 16 mm. in length—shorter than *B. infrequens.*

Our specimens are short, about 8.5 mm. long, but in other essential measurements agree with *B. infrequens,* and the scolex is so close to that figured by Hunter for this species that we identify our forms as such, notwithstanding the fact that in *toto* preparations the genitalia more nearly resemble those of *B. giganteum.* We have only four specimens of this worm, taken from three suckers, all from the mill pond at Cleveland. Hunter records this worm from *Moxostoma anisurum* only. Our records from *C. commersonnii* constitute a new host record for the species.

Biology of Caryophyllaeidae in Oneida Lake.—In this survey specimens of cestodaria were first taken during the summer of 1931, when considerable numbers of suckers from Black Creek and the mill pond at Cleveland and from the Cleveland Harbor adjacent to the mouth of Black Creek were examined. Our cestodarians came from eleven fish, nine of which were from the mill pond, and all four species of cestodarians mentioned above were found in these fish. The two infested suckers from the lake harbored only *Glaridacris confusus.* Numerous large suckers from the lake were without cestodarian parasites. It is apparent that in the locality of Cleveland, at least, cestodarian infestation of suckers centers around the mill pond. Apparently the lake, in this locality, is not a favorable habitat for the propagation of cestodarian parasites which are transmitted by means of tubificid worms as intermediate hosts. The contrasting conditions found in the mill pond and the lake would explain the difference in cestodarian infestation noted in these localities. The soft mucky bottom of the mill pond must be an ideal habitat for a heavy population of Tubificidæ, while the open lake conditions in the vicinity of Cleveland would not be favorable.

It is of interest to note that we found all of the above named four species,—*M. ingens, G. confusus, G. catostomi,* and *B. infrequens,* in the common sucker in this survey, whereas Hunter found only one of them, *G. catostomi,* inhabiting this fish. The other three species were recorded from various species of Ictiobus, Dorosoma, and Moxostoma. Apparently in the Middle West, where the Cyprinidæ and Catostomidæ are represented by numerous large forms capable of serving as hosts, these worms are rather limited in their host relationships. In the Oneida Lake area, on the other hand, where fewer members of the sucker family are found, the common sucker serves as host to all four species above mentioned,—often in mixed infestations, as, for example, *Monobothrium ingens* and *Glaridacris catostomi* which we found occurring in this way, and also *G. confusus* and *Biacetabulum infrequens.* We did not find *G. laruei* in Oneida Lake although this species has been recorded as occurring along with *G. catostomi* in mixed infestations in the common sucker in the Middle West.

We have one individual of a cestodarian from the carp, which we are not able to identify. The worm is small, but its anatomy, so far as can be determined, does not clearly coincide with any of the above species.

All of our records are from suckers taken in June and July. At that season of the year only about 25 per cent of the suckers from Black Creek and from Oneida Lake immediately adjacent to its mouth, harbored Cestodaria but all of the infestations were remarkably light.

Family Diphyllobothriidae

Ligula and Schistocephalus are two genera of cestodes which reach sexual maturity in the digestive tract of water birds. The two genera agree in the utilization of fresh-water fishes as a host before entering the avian host. Within the body cavity of the fish the post-larval tapeworm undergoes extended development and growth so that the adult stage in the bird is correspondingly shortened. Several other genera have been ascribed to this same family, and Poche (1926:352) has listed thirteen genera as the total. Only one genus belonging to this aggregate has been found in the Oneida Lake fauna. This is the genus Ligula, which has been found in the body cavity of several fishes. Schistocephalus has been reported from various points on this continent, but has not been found in Oneida Lake fishes.

Genus Ligula Bloch, 1782

The genus Ligula is represented by a single species of very general distribution in the Holarctic fauna. The adult stage, which occurs in the intestine of a wide variety of water birds, is not so commonly observed as the post-larval stage inhabiting the body cavity of fishes. All the records of Ligula in the fishes of Oneida Lake are clearly attributable to the species *L. intestinalis.*

Ligula intestinalis (Linnaeus, 1758)

Plate 35, Figures 5–6

Hosts.—Post-larval stages in the body cavity of *Boleosoma nigrum olmstedi, Perca flavescens, Hybognathus regius, Catostomus commersonnii, Micropterus dolomieu.*

In host relations this species shows very wide tolerance as indicated by the long list of fishes compiled by Cooper (1919) in his treatment of the larval stages. Infested minnows are often distinguishable because of their greatly distended bellies. The size attained in the fish host is directly correlated with the size of the host. In minnows and darters, Ligula rarely exceeds a length of five or six inches, after preservation, though the writers have observed specimens of the same species more than a foot in length taken from the body cavity of the common sucker.

According to European investigators, Ligula so nearly consummates its development in the fish host that it may begin to produce eggs within 36 hours after its introduction into the digestive tract of a bird. The adult stage is correspondingly shortened, for it has been determined that the sexually mature condition inside the bird may last only three or four days.

There is no development of functional bothria on the scolex of the larva, and though rudiments of the reproductive organs are clearly visible there is no division of the body into proglottids. The body tapers toward both ends, but the posterior extremity is much more attenuated than the anterior.

Biology of Ligula in Oneida Lake.—We have in our collections a total of 8 worms of this species from Oneida Lake. During the summer months, when our observations were being made, Ligula was found very rarely in the parts of Oneida Lake which we studied. Four worms were secured from a total of 25 specimens of *Boleosoma nigrum olmstedi*, most of which were taken by trawl in deep water off Jewell. Two specimens of fingerling perch from Cleveland and one from Lower South Bay had a single Ligula each. The records for Catostomus here given are from Chittenango Creek and Skaneateles Lake. The fact that two of the perch were very small individuals taken in deep water by trawl, and that the infested Boleosoma came from deep water, would tend to associate the larvæ of this worm with the fish species living near the bottom in the open waters. In other lakes the writers have found Ligula very frequently in schools of minnows inhabiting shallow waters of the lake shores. This parasite seems unusually rare in Oneida Lake, compared with its occurrence in other localities. Specimens in the Roosevelt Station fish collection indicate that the parasite is much more abundant in suckers in nearby smaller lakes, and that it attains a much larger size. Suckers from Cranberry Lake frequently carry Ligula over a foot in length. It is of interest to note further that whereas suckers are usually the chief host of Ligula in other waters, in Oneida Lake proper none of the 34 suckers examined carried it. On the other hand, the tessellated darter, so far as our limited records show, seems to be the chief host of the parasite in this lake, with the young fingerling perch second in incidence of infestation. However, one large sucker from near the mouth of Chittenango Creek, taken in April, 1929, was found to carry two large specimens of Ligula, almost a foot in length, so that evidently suckers do occasionally harbor the worm in these waters.

Family Bothriocephalidae

The family Bothriocephalidæ, as conceived by Poche (1926), is represented in Oneida Lake by the single genus Bothriocephalus, which occurs in the digestive tract of fishes. The genus Abothrium which Cooper assigned to the Ptychobothriidæ along with Bothriocephalus is, according to Poche's scheme, removed to the family Amphicotylidæ.

Genus Bothriocephalus Rudolphi, 1808

The genus Bothriocephalus includes tapeworms having an elongated scolex bearing two weakly developed sucking grooves, and with well marked divisions of the body into proglottids. Cooper (1919) has made a very thorough revision of this genus in which he recognizes two species as pertaining to the fresh-water fishes of North America. Both of these species (*B. claviceps* and *B. cuspidatus*) occur in the Oneida Lake fauna and a third species (*B. formosus*) has been described by the present authors (1932) on material collected from Percopsis taken in Oneida Lake.

Larval stages of Bothriocephalus, which seem to be passed in hosts unsuited to bring the worms to sexual maturity, have been found in a number of fish, as follows: *Lepibema chrysops, Esox lucius, E. niger, Catostomus commersonnii, Eupomotis gibbosus, Ambloplites rupestris* and *Leucosomus corporalis.* These hosts seem to have no significance in the life cycle of the tapeworms, and since the determination of the species on the basis of the scolex alone is difficult, no attempt has been made to give specific identifications of these specimens. This genus (Bothriocephalus) is known to have an infestive stage transmitted by copepods. Hence any fish eating copepods is exposed to periodic infestation with the young of these worms. Since at some stage of their lives nearly all fish subsist in part upon copepods, some degree of infestation with young Bothriocephalus is well nigh universal among fishes. The worms, however, have specific host relationships in that sexual maturity is attained only in certain limited host species. The larval infestations are therefore apparently insignificant with regard to host relationship, and we shall accordingly confine ourselves chiefly to a discussion of the biology of the adult worms.

Bothriocephalus cuspidatus Cooper, 1917

Plate 34, Figures 6–9

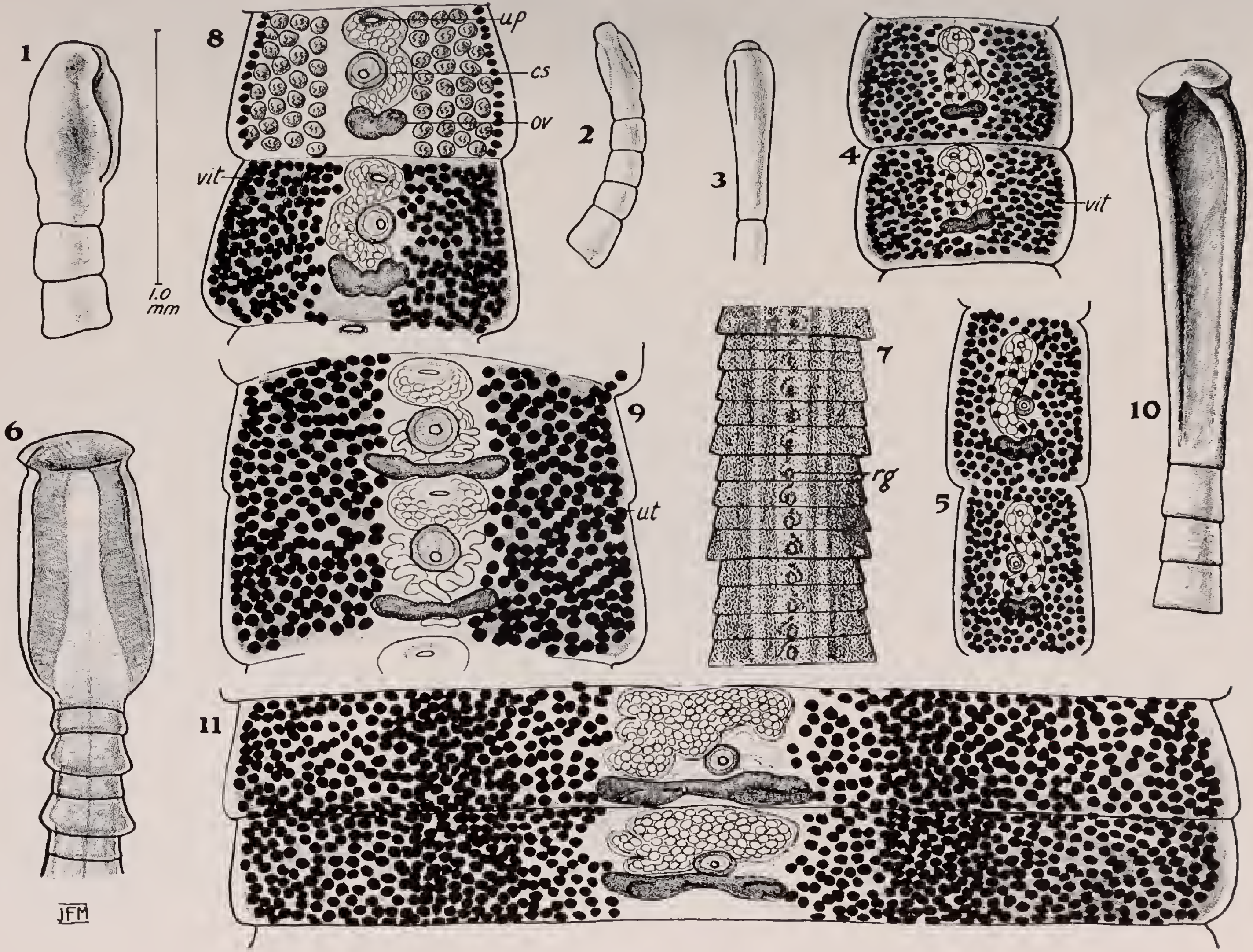
Hosts.—*Stizostedion vitreum.* In ceca and intestine.

Specimens from Stizostedion have been compared with individuals identified by Cooper as *B. cuspidatus* and have been found to agree in every detail. The most apparent difference between this species and the following are the greater width of the scolex in *B. cuspidatus,* and the greater size and width of the chain in *B. claviceps.*

At least in Oneida Lake, *B. cuspidatus* is primarily a parasite of the pike perch. In this fish it is practically always present, and frequently in great abundance, 40 or 50 adult worms to a fish. The larvæ (scoleces with a few rudimentary proglottids) are found in the intestine of a large number of fishes, but they

Plate 34. Bothriocephalus, various species. (All figures drawn to same scale as Fig. 1.) 1, 2, 3, Scoleces of *B. formosus*. 4, 5, Proglottids of *B. formosus*. 6, Scolex of *B. cuspidatus,* lateral view. 7, Young strobila of *B. cuspidatus* showing secondary fragmentation of proglottids. 8, 9, Proglottids of *B. cuspidatus,* superficial vitellaria omitted from anterior proglottid of Fig. 8 to show testes. 10, Scolex of *B. claviceps,* surficial view. 11, Two proglottids of *B. claviceps.*

cs—cirrus sac, ov—ovary, rg—rudiments of reproductive organs, up—uterine pore, ut—uterus, vit—vitellaria.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do not mature. Occasionally in the yellow perch these young worms make a slight approach toward sexual activity, but it is obvious that even in this closely related host conditions are unfavorable, for most of the worms remain undeveloped and even the largest individuals are evidently not flourishing. Cooper (1918:124) records *Perca flavescens* as a host of this worm in lakes Kegonsa and Monona, Wisconsin, but, unless this record is based upon the larval forms, the statement is not in agreement with our findings. Cooper also records *Percina caprodes* as a host of *B. cuspidatus* in Douglas Lake, Michigan. We have taken seven Bothriocephalus from this host in Oneida Lake, but these resemble our species *B. formosus,* rather than *B. cuspidatus.*

According to the observations of Essex (1928:348), the larvæ of *Bothriocephalus cuspidatus* develop in the bodies of various species of Cyclops. Since Cyclops is a free-swimming organism of the plankton, it is fairly uniformly distributed throughout the lake, hence opportunity for infesting fish through the agency of Cyclops is universal, and not restricted to particular habitats within the lake. Pike perch probably carry this species throughout the year. Our records for the summer months show practically 100% infestation with this species. Perch examined in the winter contained young larvæ, showing that possibility of infestation occurs throughout the year.

Essex (1928:352) found that after an incubation period of four to eight days a ciliated larva or coracidium hatches from the egg of *B. cuspidatus.* When coracidia were placed in water containing copepods of the genus Cyclops, the larvæ could be demonstrated within the body cavity of the copepods in two to three hours after the coracidia were introduced into the water. Various species of Cyclops were found capable of serving as host to *cuspidatus,* thus assuring a wider distribution and more abundant representation than would be possible if the host list were more restricted. After nine or ten days in the body of Cyclops, the larva is fully developed and is recognizable as the procercoid stage, which is capable of becoming established in the digestive tract of the pike perch or other suitable fish which feeds upon infested copepods.

Bothriocephalus claviceps (Goeze, 1782)

Plate 34, Figures 10–11

Hosts.—*Anguilla rostrata, M. dolomieu,* in intestine.

The eel is the only significant host of this worm in Oneida Lake. We have a single specimen of what appears to be this species from the small-mouth black bass, taken in 50 feet of water off Cleveland. This case constitutes an isolated record, as we have no other instance of the adult worm occurring in any host other than the eel. We have numerous scoleces and young post-larval worms from a variety of fishes. The white bass carries an unusually large number of what seem to be scoleces of this species. Like its near relative *B. cuspidatus,* this worm is also unable to mature in any but its proper host, which is the eel. The exceptional worm from the black bass mentioned above is without parallel, since no other author has recorded the worm from this host.

In the eel *B. claviceps* attains a length of a foot or more, and has proglottids about 3 mm. wide. The edges of the scolex are usually more nearly parallel than in *B. cuspidatus,* and the terminal disc is wider than the remainder of the scolex.

Most of the eels were examined collectively, hence records of individual infestations are not available. Considerably less than 50% of the eels in Oneida Lake are infested with *B. claviceps,* and in no instance have individual infestations been heavy.

Bothriocephalus formosus Mueller and Van Cleave, 1932

Plate 34, Figures 1–5

Hosts.—*Percopsis omisco-maycus, Boleosoma nigrum olmstedi, Percina caprodes zebra* (?); in intestine.

This species was described by the present writers in Part II of this report. The type host is the trout perch, Percopsis. In this fish it is not at all common, occurring in only about one out of every 50 fish examined. Seven Bothriocephalus from Percina and other specimens from Boleosoma appear to be this same species. All the host fishes came from deep water. No additional information is available since the original description, and nothing is known of the life history. Percopsis is an inhabitant of the deep water, roaming over the bottom in large schools. The infested Percina were taken in the trawl in 55 feet of water, off Cleveland. It is clear that this parasite belongs to the deep-water association of the lake. It is possible that Cooper's record of *B. cuspidatus* from *Percina caprodes* was really *B. formosus.*

Family Triaenophoridae

In Cooper's revision of the Pseudophyllidean cestodes of fishes of North America (1920), the genus Triaenophorus was included under the family Diphyllobothriidæ. In this he followed Lühe (1910). More recently the early proposal of Blanchard (1849) to recognize Triaenophorus as type of a distinct family has found favor with some helminthologists and has been adopted by Poche (1926).

Genus Triaenophorus Rudolphi, 1793

The genus Triaenophorus includes tapeworms of fishes which, in addition to two shallow sucking grooves, have the scolex armed with four chitinized plates, each of which has three recurved points protruding from the surface of the scolex anterior to the sucking grooves. Until recently only the immature stages in the life cycle of Triaenophorus have been known for this continent. These immature worms have been very generally recognized as of two types, parallel and presumably identical with the two species in Europe recognized as *T. crassus* (=*T. robustus*) and *T. nodulosus.*

In recent years, European investigators have restudied the genus Triaenophorus. While these recent contributions have done much toward clearing up the confusion regarding the synonymy of these forms and have added materially to an understanding of the biology of the species, some authors are still in doubt as to the validity of the distinctions drawn between the two species. Thus, Meggitt (1930:343) has stated that "The differences between *T. nodulosus* and *T. robustus* Olsson, 1893, do not seem to be of specific value."

Scheuring (1921-1928) has published a series of significant contributions dealing with details of taxonomy, biology, and distribution of the two species represented in the European fauna. Fuhrmann (1926:31) has established *T. crassus* Forel, 1880 as the valid name to replace *T. robustus* Olsson which has appeared in most of the recent literature on the genus. More recently the valid designation for the species, which has ordinarily gone under the name of *T. nodulosus,* has been brought into question. Joyeux and Dollfus (1931:110) have accepted *Triaenophorus tricuspidatus* (Bloch, 1779) to replace *T. nodulosus* (Pallas, 1791). The present writers have not examined the evidence on which this change is advocated, hence choose to use the generally accepted *T. nodulosus.*

Scheuring (1928) has raised the question as to whether differences in hook size noted for European and American specimens indicate specific differences or are merely a reflection of individual variation in response to conditions encountered within different hosts of a cosmopolitan species. Cooper (1919:82), working on the American representatives of this genus, adopted the conservative stand of referring to his material as of the "nodulosus-type" and the "robustus-type", since all of his material was immature and no adults had yet been reported from this continent. He pointed out the fact that while *T. nodulosus* becomes encysted in the liver and other viscera of its intermediate hosts, *T. crassus* passes its late larval stages in large muscular cysts within the back muscles of fishes. Scheuring (1928:159) extended observations on the latter and recorded small larvae, without cysts, within the body musculature.

Despite the objection of Meggitt, cited above, the two forms are readily separable even in the larval stages, for the chitinized hooks are characteristic for each form.

Triaenophorus crassus Forel, 1880

Plate 35, Figures 1, 3

Host.—Late larval stages in *Percopsis omisco-maycus;* location uncertain.

A number of Triaenophorus were secured from the dishes in which specimens of Percopsis had been teased to fragments. In form of the scolex and shape of the grappling hooks these larvæ are clearly of the "robustus-type" as described by Cooper and by European investigators. We have in consequence identified these as *T. crassus* (=*T. robustus*) in the belief that the parallel European and American representatives of this genus are identical.

The adult stage of *T. crassus* has not been found in any of the Oneida Lake fishes, though Hjortland (1928) found adult worms of this species in a single specimen of *Esox lucius* from a lake in northern Minnesota.

By Cooper (1919) as well as by Hjortland (1928) the larval *T. crassus* was found characteristically in muscle cysts of whitefishes. Numerous individuals of Leucichthys of Oneida Lake were examined, but cysts of this tapeworm were wholly lacking. All of the infested Percopsis were secured by means of the beam trawl operated in deep water. For a species of parasite having an alternation of two or more hosts among the fresh-water fishes, it is not surprising to find considerable flexibility in the host relationships when the geographical distribution of the parasite covers at least two continents.

Michajlow (1932:267) has found the procercoids developing in copepods. Thus the life history of *T. crassus* seems to involve a copepod as the first host, some fish as intermediate host, and a carnivorous fish (Esox) as a final host, that brings the worm to sexual maturity in its digestive tract.

While the larvæ of *T. crassus* have been most frequently reported from characteristic cysts in the back muscles of coregonid fishes, Scheuring (1928:159) has often found the larvæ lying in spaces between the muscles, with no containing cyst. It is highly probable that the liberated individuals recovered from teased specimens of Percopsis from Oneida Lake were similarly devoid of cyst walls.

Triaenophorus nodulosus (Pallas, 1781)

Plate 35, Figures 2, 4

Host.—*Stizostedion vitreum,* immature in the digestive tract.

This species differs from *T. crassus* in the form of the scolex and particularly in the shape of its chitinized tridents. The only host in which it has been found in the Oneida Lake fauna is the pike perch. It has been taken on several occasions and records include typical collecting places without any evidence of localization of areas of infestation. In every instance it has been associated with infestations of other tapeworms, chiefly of the genus Bothriocephalus. Thirteen immature *Triaenophorus nodulosus* in the intestine of a single pike perch is the heaviest individual infestation encountered. Most records are for the occurrence of from one to five worms per host.

Scheuring has (1928:157) outlined the life cycle of this species. The sexually mature worms occur in the digestive tract of Esox, while the plerocercoids are found in the viscera, especially the liver, of 34 different species of European fishes. Michajlow (1932:334) has demonstrated that two species of Cyclops (*C. strenuus* and *C. fimbriatus*) ingest eggs of *T. nodulosus* and produce normal plerocercoids.

Family Amphicotylidae

Lühe, in 1902, recognized the fundamental distinction between those bothriocephalids which have lateral openings for the cirrus and vagina and those which have these openings on the dorsal surface of the proglottids. On this basis he pointed out a true distinction between the two genera with similar scoleces, Bothriocephalus and Abothrium. Subsequent writers, including Cooper (1920:5) and Nybelin (1922:156), have recognized the validity of this distinction but have in some instances ascribed subfamily value to it and in others have attributed full family status to the two groups. The latter is the plan adopted by Poche who considers Abothrium as a genus under the family Amphicotylidæ.

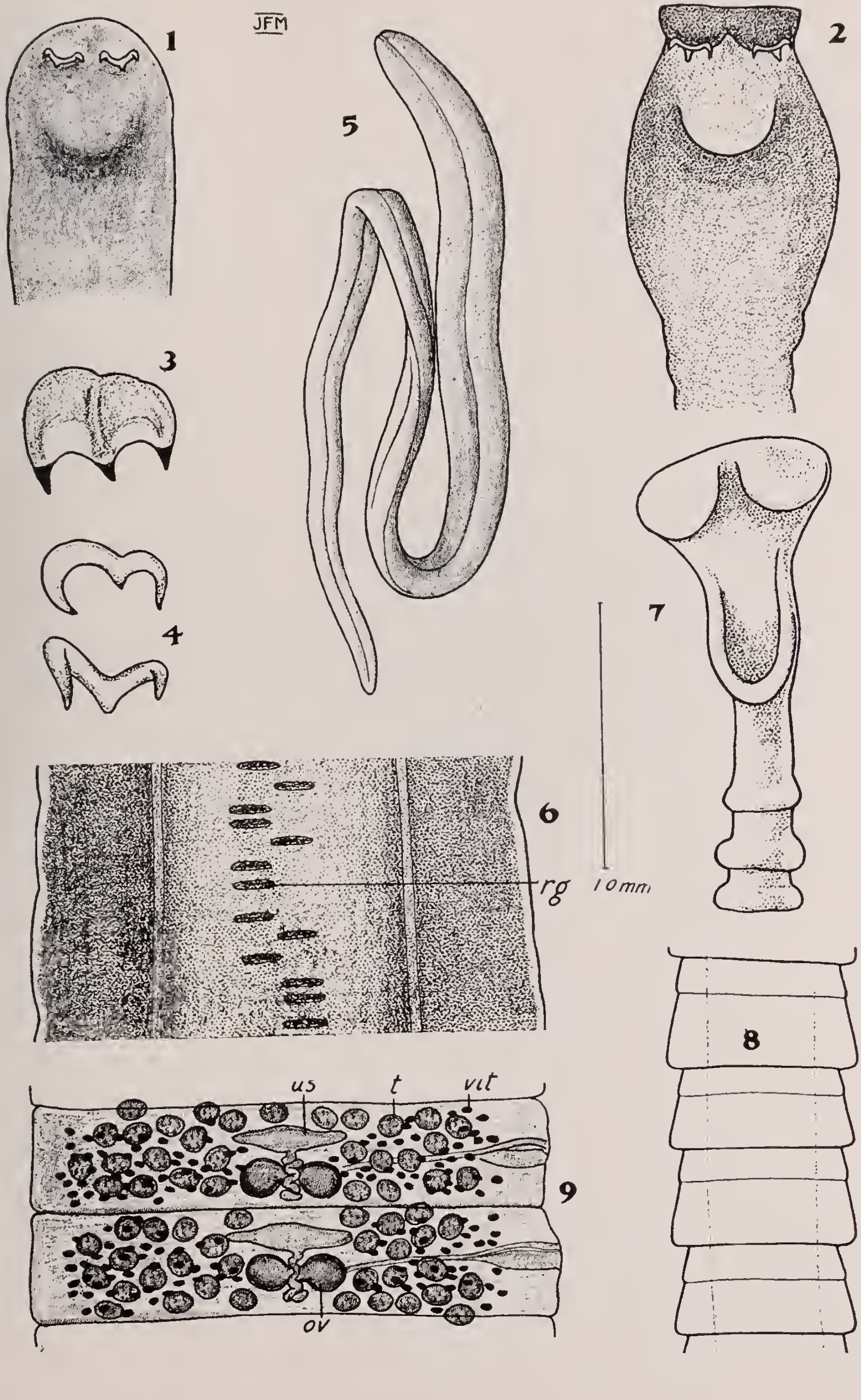
Genus Abothrium Van Beneden, 1871

The fish tapeworms belonging to the genus Abothrium have undergone radical revision within recent years. Nybelin (1922) has advocated the recognition of a genus Eubothrium to contain some of the species ascribed to Abothrium by Lühe and by American authors. Until many of the questions of synonymy and distinctions raised by Nybelin are settled by some student working with American materials, the present writers are inclined to employ the names previously used in the literature, without taking any position as to the validity of Nybelin's proposal.

Plate 35. Various cestodes. (Scale with Fig. 7 applies to all except Fig. 5.) 1, *Triaenophorus crassus,* from cysts in Percopsis, view of scolex showing hooks. 2, *T. nodulosus,* from Stizostedion, view of scolex showing hooks. 3, Hook of *T. crassus,* after Cooper. 4, Hook of *T. nodulosus,* after Cooper. 5, *Ligula intestinalis,* freehand drawing of a large specimen from a common sucker from Chittenango Creek (anterior end uppermost). 6, Appearance of cleared and stained strobila of immature Ligula from the body cavity of fishes. 7, *Abothrium crassum,* scolex. 8, *A. crassum,* immature strobila showing secondary fragmentation of proglottids. 9, *A. crassum,* mature proglottids.

ov—ovary, rg—rudiments of gonads, t—testes, us—uterine sac, vit—vitellaria.

PLATE 35



In characterizing the genus Abothrium, Cooper (1919:171) gives the following definition: "Scolex not exceptionally elongated, with two powerful but not especially deep bothria. Segmentation in older portions of the strobila usually insignificant on account of superficial wrinkling of the individual proglottides; ripe proglottides essentially broader than long. Longitudinal nerves near the lateral borders, dorsal to the cirrus sac and vagina. Testes exclusively between the nerve strands. Vitelline follicles of very irregular shape in two broad lateral fields, in part at least between the bundles of the longitudinal muscles, the follicles of individual proglottides not especially separated from one another. Ovary scarcely lobed, more or less bean- or kidney-shaped. Shell gland dorsal to the ovary. Uterus sac in ripe proglottides occupying the whole of the medullary parenchyma. The openings of the uteri correspond to a more or less prominent median longitudinal furrow of the chain of proglottides."

Representatives of the genus Abothrium have, in a number of instances, been found in the intestine of Lota from Oneida Lake. These are clearly of the species which Cooper has designated as *A. crassum.*

Abothrium crassum (Bloch, 1779)

Plate 35, Figures 7–9

Host.—*Lota maculosa,* in intestine.

Of the relatively small numbers of Lota examined, every one contained at least one specimen of Abothrium; large numbers were never present. As explained under the heading of the genus, these specimens have been identified as *A. crassum,* following the precedent of Cooper (1919:186). From the European *Lota lota,* Nybelin (1922:173) has identified tapeworms under the old specific name *A. rugosum,* but has applied a new generic name, Eubothrium. He has, in the same article, expressed the belief that the specimens of American origin from *Lota maculosa* may belong to *E. rugosum* rather than to *E. crassum,* retaining the latter name for worms parasitic in fishes of the genus Salmo.

While some of the Oneida Lake specimens have the scolex bearing a distinct mushroom-like terminal inflation such as figured by Cooper (1919: Fig. 38), others have a long narrow scolex, and still others are intermediate in form.

It seems probable that infestation with Abothrium in Lota of Oneida Lake is very general but light. Nothing is known of the developmental stages of *A. crassum* in this habitat.

Cestoda: Order Tetrarhynchidea

In his revision of the pseudophyllidean cestodes of fishes, Cooper (1920) placed his genus Haplobothrium under the order Pseudophyllidea. Poche removed Haplobothrium from this position and on characters of the scolex placed it close to the proboscis-bearing cestodes of marine fishes (the Tetrarhynchidea). In spite of pronounced morphological differences between these two groups of cestodes, the present writers are accepting the system of Poche for convenience of organization in the present report. It is entirely probable that further work may lead to a better understanding of the relationships of Haplobothrium and its assignment to a different place in the classification of the Cestoda.

Genus Haplobothrium Cooper, 1914

Cooper (1914) erected the genus Haplobothrium on the basis of secondary strobilae which have the appearance of complete worms possessing a scolex similar to the simpler scoleces in the more primitive tapeworms. Subsequent observations revealed the fact that the worms originally described are the result of secondary asexual fragmentation of the primary chain and that the primary strobila bears a highly differentiated scolex with four eversible proboscides similar to those found in the Trypanorhyncha, but lacking hooks. The organ originally described as a scolex is but the slightly modified anteriormost proglottis of each secondary fragmentation product. The secondary or pseudo-scolex is provided with shallow dorso-ventral depressions analogous to the bothria of Bothriocephalids.

A single species, *H. globuliforme,* has been assigned to this genus. So far as published records go, the only host of the adult of this species is *Amia calva.* No specimen of this fish has been taken by us in Oneida Lake, but larvæ of Haplobothrium were found encysted in the liver of a sunfish collected near Brewerton. The evidence would seem to necessitate the presence of Amia to provide the eggs from which the larvæ in the sunfish could develop. An Amia specimen from Cross Lake, about 25 miles distant from Oneida Lake was examined and the mature primary strobilæ of Haplobothrium obtained from it were included in the present study. The specimens from this source agree in all respects with the description of *Haplobothrium globuliforme* and have here been recognized as such.

Haplobothrium globuliforme Cooper, 1914

Plate 36, Figures 1–4

Hosts.—*Amia calva,* in intestine. Larva encysted in liver of *Eupomotis gibbosus.*

Essex (1929) and Thomas (1930) have worked on the life cycle of this species. Essex described larvæ from the liver of *Ameiurus nebulosus.* Thomas recorded experiments wherein larvæ of Haplobothrium were obtained experimentally by feeding the eggs and young larvæ to Cyclops. The same author reports an instance of the occurrence of larvæ encysted in the liver of a sunfish. The four long, eversible proboscides on the primary scolex of this worm readily differentiate it from all other cestodes found in fresh waters of this continent. Both the scolex and the mature proglottides of the worms from Amia from Cross Lake agree in all essential details with the description given by Cooper (1919:44).

The cestode larvæ recorded by Pearse (1924:176) as Trypanorhyncha of undetermined genus and species, are very probably the larvæ of Haplobothrium. Pearse's records were based upon visceral cysts found in the "yellow bass, skipjack, and top minnow" of Wisconsin lakes.

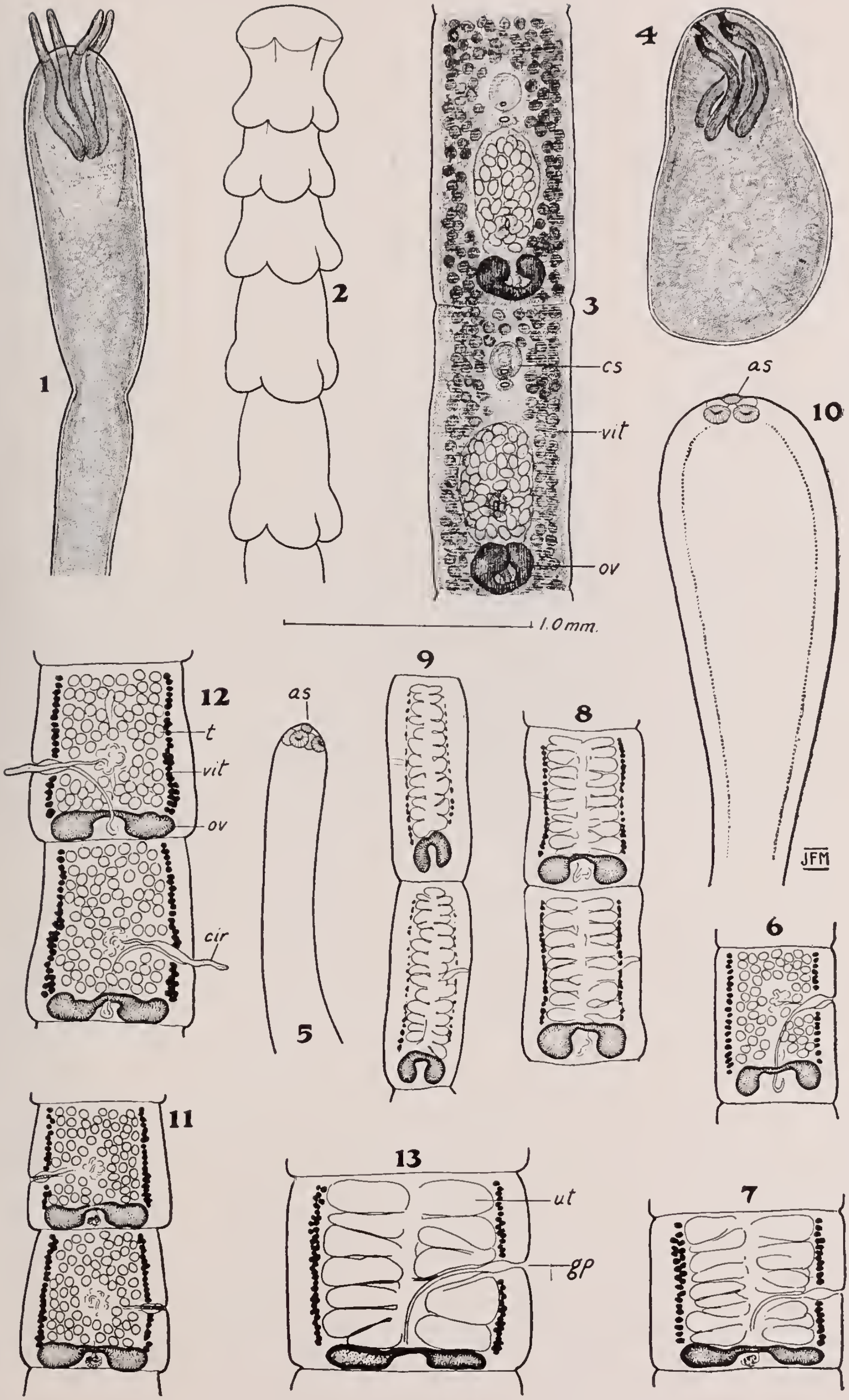
Cestoda: Order Taeniidea

According to Poche (1926:366) the highest cestodes comprise an order to which the name Taeniidea has been ascribed. As adult tapeworms in fresh-water fishes, only two genera representing this order have been found in Oneida Lake; these are the genera Proteocephalus and Corallobothrium, both of which belong to the family Proteocephalidæ.

Plate 36. Various cestodes. (All Figures drawn to same scale.) 1, *Haplobothrium globuliforme,* primary scolex. 2, Pseudo-scolex and young proglottids. 3, Mature proglottids. 4, Larva from liver of sunfish. 5, *Proteocephalus pearsei,* scolex. 6, 7, 8, 9, *P. pearsei,* proglottids in various stages. 10, *P. pinguis,* scolex. 11, 12, 13, *P. pinguis,* proglottids in various stages.

as—apical (fifth) sucker, cir—cirrus, cs—cirrus sac, gp—genital pore, ov—ovary, t—testes, ut—uterus, vit—vitellaria.

Plate 36



Family Proteocephalidae

LaRue (1911) recognized the family Proteocephalidæ as a group of genera reaching maturity in fresh-water fishes, amphibia, and aquatic reptiles. The small scoleces in these forms bear four sessile suckers and may have a terminal fifth sucker at the tip of the scolex, but this organ shows all degrees of development and degeneration. In some species it is functional and in some wholly wanting, and between these extremes it presents varying degrees of development.

In Oneida Lake fishes but two genera representing this family have been found—Proteocephalus and Corallobothrium.

Genus Proteocephalus Weinland, 1858

The extensive monograph by LaRue (1914) furnished for American workers an admirable treatise on the Proteocephalidæ. The genus Proteocephalus is more widely represented in the Oneida Lake fauna than any other genus of tapeworms. This statement holds both for the number of species represented and for the numbers of individuals present. The following generic diagnosis is adapted from LaRue (1914:12).

Generic diagnosis.—Head globose or conical, flattened dorso-ventrally. No rostellum. No spines or hooks. No fold of tissue encircling base of head or enfolding suckers. Suckers circular or oval. Fifth sucker functional, vestigial, or lacking. Testes in a broad field between vitellaria. Parenchyma with close meshes. Musculature well developed. Eggs with three membranes.

Habitat: In fresh-water fish.

Five species of Proteocephalus have been found in the fishes of Oneida Lake. The larval stages of some of these are distinguishable with the greatest difficulty, but mature chains are rather easily identified by means of the following key.

Key to the Species of Proteocephalus Found in Fishes of Oneida Lake

1	(a)	Fifth sucker present at tip of scolex	2
	(b)	Fifth sucker lacking	4
2	(a)	Broad spatulate head well set off from long slender neck	**P. pinguis**
	(b)	Head small, not set off from neck	3
3	(a)	Small worms, not over 50 proglottides	**P. pearsei**
	(b)	Large worms, with 150 proglottides or more	**P. macrocephalus**
4	(a)	Testes 70–100 in each proglottis	**P. amploplitis**
	(b)	Testes 130–150 in each proglottis	**P. perplexus**

Proteocephalus pinguis LaRue, 1911

Plate 36, Figures 10–13

Hosts.—*Esox lucius, Esox niger;* in intestine.

According to LaRue, this species is widely distributed in North America. Hunter has reported it from various localities in New York State. In our Oneida Lake collections this is the only species of tapeworm present in either *Esox lucius* or *E. niger.* It is readily distinguishable from the related *P. pearsei* by its large size, more numerous proglottides, and spatulate head at the end of a very slender neck.

The parasite is present in practically 100% of the *E. lucius* in Oneida Lake and this fish must be regarded as its chief host. Very heavy infestations occur, the number in a single fish frequently being so large as almost to occlude the intestine. We have taken as many as 100 worms from a single fish.

In *E. niger,* infestations are scarcer and lighter. In this host incidence is only about 25%, and seldom are more than one or two worms found in a single fish. *E. niger* taken through the ice in winter also harbored the worm.

The fish bearing this parasite were taken from a variety of shallow-water habitats, indicating a general infestation of pike and pickerel. Both of these fishes in Oneida Lake are found inhabiting the protected shore waters.

Hunter (1929:487) has worked on the life history of *Proteocephalus pinguis,* and found *Cyclops vulgaris* and *Eucyclops agilis* capable of artificial infestation. These and other copepods doubtless serve as the first host of the larval *P. pinguis.* Hunter (1929:494) has further found that various fishes may serve as intermediate host for *P. pinguis,* conveying it between the crustacean primary host and the digestive tract of Esox. Young yellow perch were found especially susceptible to experimental infestation by plerocercoids of this worm. On the basis of field and experimental data, Hunter (p. 494) has expressed the belief that Esox may become infested with *P. pinguis* either through feeding on its crustacean host, or through the agency of other fishes which acquire the tapeworm larvæ from the crustacean host. Such an alternative method would readily explain the general infestations found in *Esox lucius,* for two links in the food chain rather than a single group of food organisms contribute to the building up of a general infestation.

In accordance with the above, the larvæ of this worm, as in the case of other cestodes, are occasionally found in the intestine of fishes incapable of bringing the parasites to maturity. The larvæ are difficult to identify, however, because of their similarity to the young of *P. pearsei,* with which they may easily be confused. Hence we do not submit any list of hosts for this larva.

Proteocephalus pearsei LaRue, 1919

Plate 36, Figures 5–9

Hosts.—*Perca flavescens, Lepibema chrysops,* in intestine.

Like *P. pinguis,* this worm bears a fifth sucker. Its small size, fewer proglottides, and narrow head continuous with the neck, however, set it off from the latter species. The worm is not common in any host. Only a small number—less than 10 per cent—of the perch were infested with it. It occurs also in the white bass, but infested fish of this species were fingerlings two to three inches in length. The infested perch came in about equal numbers from deep- and shallow-water habitats, which concurs with the general distribution of copepods carrying the infestive stages. The infested white bass were from deep water, the only habitat from which fingerlings of this species were taken. Six large *L. chrysops* from Billington's Bay did not contain the worm.

The larvæ are occasionally found in *Stizostedion vitreum, Micropterus salmoides,* and others, but do not mature in these hosts.

This form was not recognized and distinguished as a separate species at the time when LaRue prepared his comprehensive monograph of the genus (1914). In studying the life history of *P. pearsei,* Bangham (1925:257) discovered facts which tend to explain why this species was not discovered at an earlier date. Larvæ of *P. pearsei,* according to Bangham, develop in both copepods and cladocerans, and at least in the instance of the black bass are transferred directly to the definitive host when plankton crustacea containing the plerocercoid larvæ are taken as food. In the fish host, *pearsei* matures quickly. Since only the young of most fishes feed exclusively on plankton organisms, this tapeworm is especially prominent in very young fish. In most of the worms the life cycle is completed so that they are not carried by the fish host beyond the first season. Thereafter, plankton organisms play less prominent roles in the food chains, with the consequence that *P. pearsei* is a less conspicuous inhabitant of the digestive tract in older fish. In contrast with this, stand some other species of Proteocephalus in which the larval tapes within the crustacean host become established as advanced larvæ in other fishes, which in turn transfer the tapeworms to the final fish host. In the latter instance the time of infestation of the definitive host is not restricted to the period when this host is a plankton feeder, but extends throughout the life of the fish.

Proteocephalus macrocephalus (Creplin, 1825)

Plate 37, Figures 4–5

Hosts.—*Anguilla rostrata, Stizostedion vitreum;* in intestine.

This species is a worm of fair size, 10 cm. or more in length, and 1.5 mm. to 2.0 mm. in width. It is the only species of Proteocephalus found mature in the eel. Only about 30 per cent to 40 per cent of the eels carry the parasite, and in small numbers, two or three worms to a fish.

The pike perch has been found in one instance to contain an adult worm which, so far as could be determined from the mounted specimen, also belongs to this species. This worm was not so long as the *P. macrocephalus* from the eel, but agreed with it in essential structural characters. This is an isolated case. What appear to be larvæ of this worm have also been taken from the pike perch on several occasions. Pratt (1923:64), in his earlier survey of Oneida Lake fish parasites, records two species of Proteocephalus from the eel, a large and a small one. A restudy of his material has revealed that he had both *Bothriocephalus claviceps* and *Proteocephalus macrocephalus.* Evidently he confused *B. claviceps* with *P. macrocephalus,* for he does not record *B. claviceps* as present and only the one species of Proteocephalus was found in his vials.

So far as the present writers have been able to determine from the literature, nothing is known of the life cycle of *P. macrocephalus.*

Proteocephalus perplexus LaRue, 1911

Plate 37, Figures 8–9

Host.—*Amia calva;* in intestine.

Our material of this species came from Cross Lake. We have not taken the host, *A. calva,* in Oneida Lake, although we have evidence that it occurs there.

This worm is easily distinguished from other species of Proteocephalus by characters given in the table. The worm is of fair size, about 10 cm. long, and about 1.5 cm. wide.

This species was originally described from *Amia calva* and *Lepisosteus platostomus* from the Illinois River (LaRue, 1914:479). More recently Pearse (1924a: 176) has recorded it from a number of hosts in Wisconsin Lakes, and has found visceral cysts in the white bass, bullhead, and blunt-nosed minnow. Full details of the life cycle do not seem to be available.

Proteocephalus ambloplitis (Leidy, 1887)

Plate 37, Figures 6, 7, 10

Hosts.—*Micropterus dolomieu, M. salmoides;* in intestine.

The adult worm is large and robust, about 10 cm. in length by 2.0 mm. in width. It has been recorded from *A. rupestris, M. salmoides* and *Amia calva* in other waters. The larva occurs encysted in the mesenteries and viscera of numerous fishes. We have taken it from *M. dolomieu, P. flavescens, B. nigrum olmstedi, I. punctatus, A. rupestris, E. gibbosus, E. niger, A. nebulosus,* and others. The larva is a whitish grub about 10 mm. long, and in cleared mounts shows a spherical, deeply staining terminal organ, supposed by some to represent the fifth sucker of certain other proteocephalids. The head is expanded and separated from the body by a furrow. These larvæ have been known to cause economic loss as a result of becoming established in the gonads of hatchery black bass. In such case, if these larvæ are numerous, the gonad becomes fibrous and the fish is unable to spawn.

Moore and Hunter have done considerable work on this parasite in New York hatcheries. Bangham has shown similar losses in Ohio where he attributes (1927: 214) the small percentage of *Micropterus dolomieu* spawning in the hatcheries to infestation of the gonads by larval *P. ambloplitis.* In another paper the same author (1927b:206) refers to *P. ambloplitis* as "a most serious handicap to the hatching of bass."

Hunter (1928:239) found *Cyclops albidus, C. prasinus, C. leuckarti,* and *Hyalella knickerbockeri* capable of serving as host for the development of the larva. Hunter and Hunter (1929:198) have added other species to the list of copepods capable of serving as first host, and experimentally infested several species of fish with the larvæ. At least in some instances the fish as a second intermediate host seems essential in the life cycle of the parasite here discussed.

Larval Proteocephalus

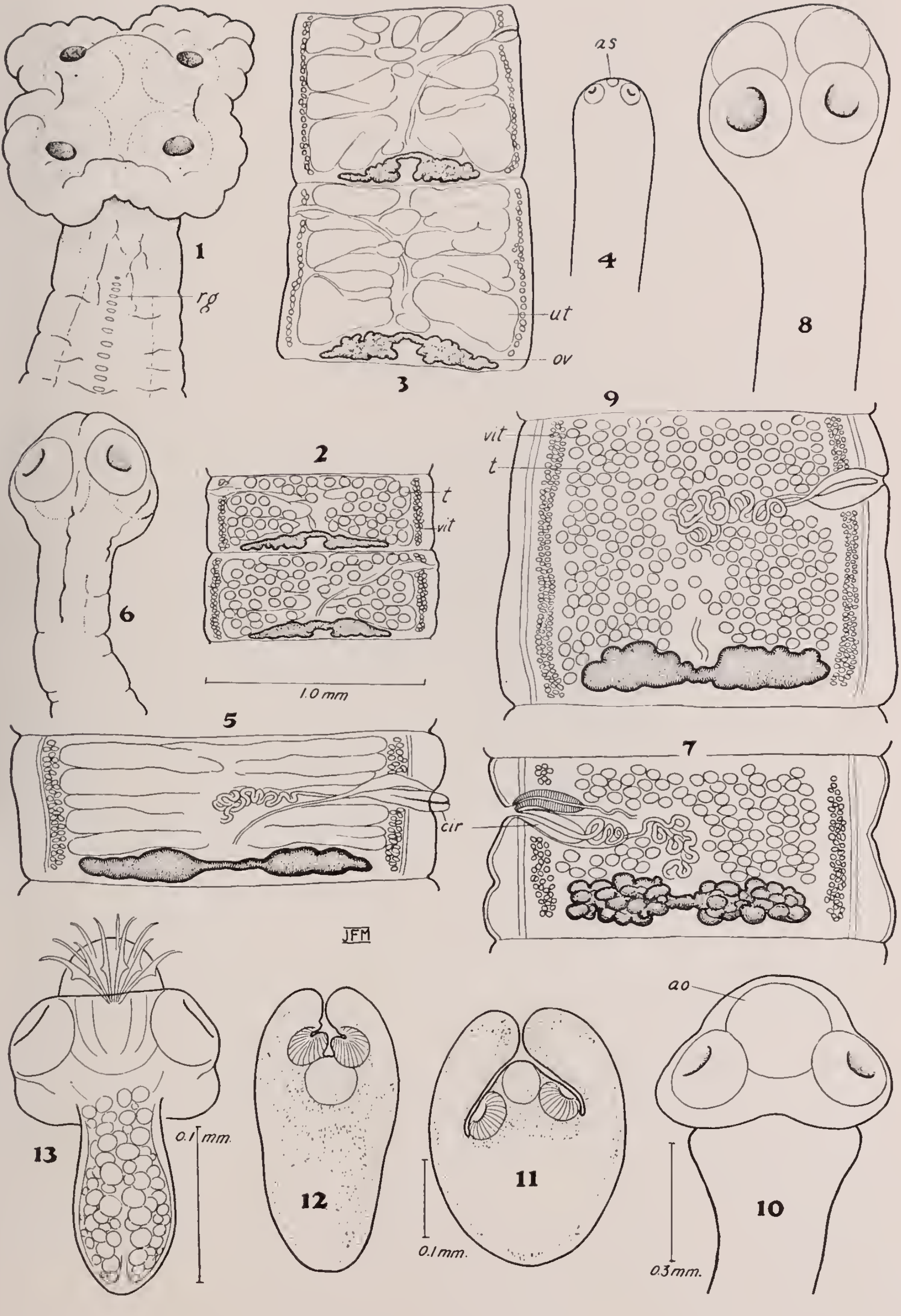
In a survey of this sort, young post-larval Proteocephalus are frequently encountered in the intestines of fishes. Most of the larvæ are encountered in fish hosts evidently incapable of bringing them to maturity. All fish feeding upon copepods must occasionally take in these larvæ, and the infestation becomes significant only when the combination of host and larva happens to be biologically appropriate.

Some of our larval proteocephalids were tentatively identified, while others remain questionable. The larvæ of *P. pearsei* and *P. pinguis* are easily confused,

Plate 37. Various cestodes. (Figures 1–9 drawn to scale shown with Fig. 2.) 1, *Corallobothrium fimbriatum,* scolex and immature proglottids, from *A. nebulosus.* 2, 3, *C. fimbriatum,* proglottids in different stages. 4, 5, *Proteocephalus macrocephalus,* scolex and ripe proglottid. 6, 7, *P. ambloplitis,* scolex and ripe proglottid. 8, 9, *P. perplexus,* scolex and ripe proglottid. 10, *P. ambloplitis,* larva from mesenteries of bass. 11, 12, Larval *Proteocephalus* sp. from mesenteries of *Umbra limi.* 13, *Hymenolepis* sp. from gut of *M. salmoides.*

ao—apical organ, as—apical (fifth) sucker, cir—cirrus, ov—ovary, rg—rudiments of gonads, t—testes, ut—uterus, vit—vitellaria.

Plate 37



1
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3
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12
11
0.1 mm.
10
0.3 mm.

both having a fifth (apical) sucker, as has also the larva of *P. macrocephalus*. Larvæ of this type have been found in a number of fishes, including *Micropterus salmoides*, *Esox niger*, *Perca flavescens*, etc.

We found larval cestodes without an apical sucker in *P. flavescens*, *M. salmoides*, *Stizostedion vitreum*, and others.

We have also in several cases found a larva of this latter type, but with edges of suckers somewhat scalloped, from the intestine of Lota, but whether this is an abnormal form of some familiar species or a new form, we do not know. We have no adults with suckers of this type.

Larval *P. ambloplitis* occur commonly encysted in the viscera of a great many fishes. They are easily distinguished by their large size and peculiar apical organ.

Genus Corallobothrium Fritsch, 1886

This genus is distinguished from the other Proteocephalidæ by means of the following characters, taken from LaRue (1914:13).

Diagnosis: With characters of the family. Scolex with four suckers situated on the flat anterior face of the head. Many irregular folds and lappets of tissue about margin of anterior surface; may enclose suckers as in a corolla. No rostellum. No hooks or spines. Neck broad, short. Habitat: In Siluridæ.

Two species of Corallobothrium have been described from silurids of this continent by Essex, 1927. These may be distinguished by the following key:

Key to Species of Corallobothrium Reported From North America

(An asterisk denotes species found in the Oneida Lake fauna.)

(a) Scolex with large marginal fimbriae or lappets forming a pronounced collar, proglottides broader than long, ovary a linear band near posterior margin of proglottis .... **C. fimbriatum***

(b) Fimbriated collar of scolex less developed, mature proglottides longer than broad, ovary butterfly- or H-shaped .... **C. giganteum**

In our collections the genus is represented by the single species, *C. fimbriatum*.

Corallobothrium fimbriatum Essex, 1927

Plate 37, Figures 1–3

Hosts.—*Ameiurus nebulosus*, *Ameiurus natalis*, *Schilbeodes gyrinus*, *Ictalurus punctatus*; in intestine.

This worm is usually small, around 2 cm. or 3 cm. in length, although its size is to some extent correlated with that of the host. In a small host such as *S. gyrinus* we have mature strobilae about 1 cm. long. We also have worms as much as 5 cm. long from *A. nebulosus*. For some reason not apparent, fully developed worms were seldom found, most of our material being scolices with a very short chain of proglottides. Even these small worms are mature, however, for proglottides not more than 1 cm. removed from the head already contain eggs. Frequently the entire strobila in these short mature worms does not number over 50 proglottides. Our largest material consists of three worms taken in May in a bullhead from a branch of Chittenango Creek. These worms have about 100 proglottides or more, and toward the middle of the chain the links become longer than broad, in contrast with proportions found in the smaller specimens. All of our specimens from Ictalurus are small, and the strobila unsegmented, as though this host were unsuitable for the worm, although Essex reports Ictalurus as a host to both species of the genus.

Data gathered by Essex for the northern Mississippi River, Rock River and Illinois River, showed a variation in seasonal abundance. "The adult form of Corallobothrium appears in the late spring or early summer, reaches its maximum during June and July, and disappears entirely the latter part of October or the first part of November."

The life history has been worked out by Essex who found experimentally that *Cyclops bicuspidatus, C. serrulatus,* and *C. prasinus* will ingest the eggs of *Corallobothrium fimbriatum*, and that plerocercoid larvæ develop within their bodies in twelve to fourteen days after the eggs are eaten. His further experiments indicate that catfishes may secure their infestations of *C. fimbriatum* either by feeding on Cyclops bearing the procercoids or by feeding on minnows which have become infested by eating infested Cyclops. Thus the life cycle may involve either a single larval host, a copepod, or two larval hosts one of which is a fish serving the final host as food.

Family Hymenolepididae

The Hymenolepididæ are tapeworms which reach maturity in mammals and birds. The scolex, in addition to its four rounded suckers, possesses a terminal rostellum upon which is borne a distal crown of prominent hooks arranged as a single circle of eight to forty-six hooks. Each proglottis normally bears from one to four testes.

A single larval specimen, apparently of this family, has been found among the fish parasites of Oneida Lake. This specimen has been tentatively assigned to the genus Hymenolepis though its standing here remains uncertain.

Hymenolepis sp. ?

Plate 37, Figure 13

Essex (1932:291) has described and figured a larval Hymenolepis which he found in the body cavity of *Diaptomus oregonensis* from Long Lake, near Ely, Minnesota. In recording the finding of this larva, Essex has tentatively identified it as *Hymenolepis cuneata* Mayhew, 1925, a species which reaches sexual maturity in a wild duck.

In the course of the Oneida Lake survey, the present writers encountered a single larval specimen of what seems to be another species of Hymenolepis, in the digestive tract of *Micropterus salmoides*. All evidence seems to point to this as an abnormal host and location. It is highly probable that the larva is carried normally by some crustacean through whose agency the tapeworm enters a natural bird host.

Total absence of proglottides precludes exact identification of this specimen. However, the rostellar hooks are distinctly smaller than those described by Mayhew for *H. cuneata,* and by Essex for his larval form ascribed to that species.

Likewise, ten hooks are present on the rostellum while eight or less have been cited as characteristic of *H. cuneata* by Mayhew (1925:46).

Aside from the Ligula discussed in another section of this paper, the present record of *Hymenolepis* sp. ? is the only instance of either a mammalian or avian cestode encountered in the fishes of Oneida Lake.

SECTION 4. TAXONOMY AND BIOLOGY OF THE NEMATODA OF ONEIDA LAKE FISHES

The Nematoda are commonly known as round worms or thread worms. The members of their class have an elongate, cylindrical or spindle shape, and lack segmentation and the splanchnic layer of mesoderm. An elastic, hyaline "cuticula" covers the external surface and this may be entirely smooth, marked with very fine transverse annulations, or set with knobs, spines or ornaments of various sizes and forms. Unlike the flatworms the sexes are separate, and the female is usually somewhat larger than the male. At times (as in the Filarioidea) the male is minute, and in some species only the female is known. The male usually possesses a spirally coiled tail adapted to encircling the body of the female during copulation. The male genital and alimentary systems open by a single pore, the anus, near the caudal extremity. A short distance inside the anus, on the ventral surface of the cloaca, in the male, is the opening of the ejaculatory duct which transmits the sperms into the cloaca at the time of copulation. About opposite this opening, on the dorsal wall of the cloaca, open the spicule sheaths. The spicules are two chitinous, curved organs which may be needle-like, flattened into the form of ribbons, or curved into gutters or troughs. They may be equal or very unequal in length, and similar or widely different in form. In some cases an accessory piece or guide, the "gubernaculum," is present. The spicules are exserted during copulation but their exact function is not understood, for in most cases their form is clearly unsuited for conveying the sperms. A single testis is present.

The female usually possesses a straight, tapered tail. In this sex the reproductive system opens separately from the alimentary canal. The vulva, variable in position, frequently lies near the middle, seldom at the tail end. Within the vulva is frequently found a muscular bulb or sphincter called the ovejector. A short vagina branches into a bicornuate uterus, although in some cases a single uterus is present and in others more than two. The reproductive system is tubular in plan with the linear ovary at one end and the tubular uterus at the other.

The number of ovaries corresponds to the number of uteri. The female system is said to be single, double, multiple, etc., according to the pattern of duplication.

Nematodes may be either oviparous or viviparous. Egg-laying is most common, but the viviparous habit is highly developed among the tissue-parasites of the group Filarioidea. In these worms the uterus becomes greatly inflated and fills the whole body of the worm. Within swarm myriads of minute, wriggling embryos. Frequently in these worms the entire alimentary canal, and even the vagina, becomes atrophied and disappears in the adult stage so that the worm is merely a sac of living embryos.

Sensory organs occur in the form of papillæ which appear as small knobs or bosses, arranged in a definite pattern on the head and lips of both sexes and on the tail of the male. Lateral fins or folds of cuticula, known as wings or "alæ" may occur along the sides of the head, but especially on the tail of the male. In some species (Cucullanidae) the tail of the male is provided with a sucker.

The Class Nematoda is very large and comprises both free-living and parasitic forms. The free-living forms are all minute, and occur in soil, water, etc. Some are parasites of plants, in which they produce a number of important diseases, and many of these nematodes are serious agricultural pests. Parasitic nematodes occur widely throughout all groups of animals, and an immense number have been described, most of which are as yet very imperfectly understood. This lack of information is reflected in the shifting and unsatisfactory classifications of the Nematoda which have been made to date.

Parasitic nematodes show great variety in their life histories. The pattern varies from the simple type with direct transmission to that in which intermediate hosts are employed. This diversity in life histories indicates that the parasitic nematodes are not such a closely unified group as either the trematodes or the cestodes, but have probably arisen independently at a number of different points from their free-living ancestors. Structural considerations bear this out, as does also the fact that the nematodes have not as yet become so thoroughly adapted to the parasitic habit as have the flatworms. The flatworms show marked and even extreme degeneration as a result of the parasitic habit, as for instance the lack of all trace of the alimentary canal in cestodes, and the interpolation of multiple reproductive cycles into the life history to compensate for the hazards of the parasite mode of life.

The nematodes, with the possible exception of the Filarioidea, show no such wide departure from the structural plan of their free-living relatives and do not have embryonic reproductive cycles. Thus from a single nematode egg a single nematode arises; whereas from a single trematode egg, and from the egg of some cestodes, thousands of individuals may arise.

As parasites of fishes, this group is not so heavily represented in Oneida Lake as the trematodes, but ranks about equal with the cestodes. However, several of the species were found to be extremely abundant and came to our attention as often as or oftener than any other parasite.

Because of imperfect knowledge of the structure of many nematodes, a satisfactory system is hardly possible at this time. Shifts of genera to new families are being constantly made as further knowledge sheds light on their true affinities. Therefore any system at present is largely tentative. A number of large, clearly related groups, stand out in any taxonomic scheme for the parasitic nematodes, and according to the systems of different authors, these are given the rank either of orders, or of superfamilies. For the purposes of the present report we follow the scheme of Yorke and Maplestone (1926), as far as possible. However, to bring the system of classification of the nematodes more closely in harmony with the system here adopted for the flatworms, the superfamilies of Yorke and Maplestone are elevated to orders. Herein the ordinal concepts which we have adopted agree more closely with those set forth by Baylis and Daubney (1926).

Nematoda: Order Trichuroidea

Definition: Very delicate, thread-like worms, anterior portion of body filiform, esophagus a delicate capillary tube passing to one side of a chain of large single cells (para-esophageal cells). Male: spicule single or absent. Female: one ovary.

Family Trichuridae

Distinguished from its relatives by the males having a spicule or copulatory sheath. Under this family the subfamily Capillariinæ is distinguished by the character of the body, which has the anterior part shorter than or at most equal to the posterior part, which is only slightly thicker. Under the Capillariinæ belong our two species, *Capillaria catenata* and *Hepaticola bakeri.*

Prior to the description of *Capillaria catenata,* Pearse (1924) had described *C. catostomi* from Wisconsin, but other records of the occurrence of this genus in North American fresh-water fishes are lacking. That invasion of the fish host is not purely accidental is supported by records from other continents that have been appearing in the recent literature. Thus Hesse (1923:65) described *C. leucisci* from minnows caught in Loch Lubnaig, Scotland, and called attention to the bacillary bands, two highly characteristic longitudinal structures bearing wart-like prominences, which are wholly wanting in *C. catenata.* In 1927, Travassos (1927: 215) described what he designated as the first species of Capillaria from fresh-water fishes of the Brazilian fauna. Travassos' figures as well as his description show many points of distinction between *C. catenata* and the South American *C. setinosa.*

Key to the Species of Capillariinae From Fresh-water Fishes of North America

(An asterisk denotes species found in the Oneida Lake fauna.)

1 (a) Male with copulatory spicule...Capillaria. –2
(b) Male without spicule but with eversible copulatory sheath..Hepaticola....**H. bakeri***
2 (a) Para-esophageal series contains about 40 cells......................**Capillaria catenata***
(b) Para-esophageal series contains about 187 cells..................**Capillaria catostomi**

Genus Capillaria Zeder, 1800

Definition: Capillariinæ. Body capillary; mouth simple; cuticula with or without "bacillary bands." Oesophageal portion shorter than, or rarely equal to, the posterior portion. Spicule long and slender, with a protrusible sheath, the outer surface of which, when protruded, may be either smooth or spiny. Eggs barrel-shaped with polar plugs.

Capillaria catenata Van Cleave and Mueller, 1932

Hosts.—*Eupomotis gibbosus, Ambloplites rupestris, Micropterus salmoides* and *Stizostedion vitreum;* in intestine.

This was the only Capillaria found in the present survey. It has been described in Part I, and no further information has come to hand at this writing. The females are about 10 mm. to 15 mm. long with a maximum diameter of 0.055 mm., and have about 40 para-esophageal cells. The eggs are 0.055 mm. x 0.030 mm. The males smaller than the females, with spinose spicule sheath.

Genus Hepaticola Hall, 1916

Definition: Capillariinæ. Body capillary, mouth simple, cuticula without bacillary band. Spicule absent, but a membranous eversible sheath present. Female, anterior portion of body half as long as posterior portion. Eggs with polar plugs, and striated shell.

Hepaticola bakeri Mueller and Van Cleave, 1932

Hosts.—*Leucichthys artedi tullibee, Notemigonus crysoleucas, Catostomus commersonnii;* in intestine.

This is the only species of Hepaticola in our Oneida Lake collections. It has been fully described and figured in Part II. Contrary to the recorded habitat of the genus (liver of mammals) this species is found in the intestine of fishes. The para-esophageal series numbers 38 to 40. The female measures about 7 mm. in length, the male about 4.5 mm. This is the only member of the genus to be reported from a fish.

Biology of Capillariinae in Oneida Lake. Both *Capillaria catenata*, and *Hepaticola bakeri* are of infrequent occurrence. *C. catenata* occurs most often in the common sunfish, which is probably its natural host. *H. bakeri* seems less common than its relative and was found oftenest in the tullibee. It is of interest to note that *C. catenata* occurred in four different species, all of them hard-bodied game fishes. *H. bakeri* in contrast, occurred in three species of fish, but all of these were soft-bodied "cull fishes." This difference in host relationship must reflect some feature in the life history of the worms.

Nematoda: Order Ascaroidea

Definition: Usually fairly large and stout. Head with three prominent lips, one dorsal, two subventral. Interlabia present or absent. Esophagus with or without posterior ventriculus. Esophageal and intestinal ceca may be present or absent.

Two families may be distinguished by the character of the alimentary canal as follows:

Ascaridae: with a simple alimentary canal, without esophageal or intestinal diverticula.

Heterocheilidae: alimentary canal not simple, with a post-esophageal ventriculus and/or esophageal and intestinal diverticula.

Family Heterocheilidae

The Heterocheilidæ are divided into several subfamilies, of which the Anisakinæ are distinguished by the lack of cuticular spines or other raised structures. The Ascaroidea which have up to this time been described from North American fishes fall into this subfamily, the Anisakinæ.

Genus Contracaecum Railliet and Henry, 1912

Definition: Anisakinæ. Interlabia present, usually very well developed; dentigerous ridges absent; esophagus with a reduced posterior ventriculus, giving off a solid posterior appendix; intestinal cecum present. Male: without definite caudal alæ; three or four pairs of post-anal papillæ which may be doubled, and numerous pre-anal papillæ; spicules equal; gubernaculum usually absent. Female: vulva in the anterior part of the body. Oviparous.

A large nematode from the stomach and intestine of the large-mouth black bass and the rock bass is abundantly represented in the Oneida Lake collections. These worms are readily assignable to the genus Contracæcum. In some specimens, the anterior cecum, arising from the intestine, is recognizable only with difficulty, but in many individuals it is easily observed. (See Plate 38, fig. 5). The presence of this cecum is the only significant point wherein these specimens differ from the description of *Hysterothylacium brachyurum* Ward and Magath, 1917. Adhering to the belief that fundamental agreement in practically all other points of morphology and in host relationship justifies an assumption of identity, the present writers maintain that the specimens under consideration are compatible with an emended concept of *H. brachyurum.*

The original description of *H. brachyurum* was based exclusively upon small males, for no females were included in the type material. A size of 32 mm. is cited as the length of a male by Ward and Magath, while some of our males reach 60 mm. and females attain a length of 90 mm.

The status of the genus Hysterothylacium has been in dispute. Yorke and Maplestone (1925:274) and Baylis and Daubney (1926:4) have submerged this name as a synonym of Raphidascaris. The present writers are not prepared to propose that Raphidascaris be regarded as a synonym of Contracæcum, but suggest that Hysterothylacium should be regarded as a synonym of Contracæcum rather than of Raphidascaris. In consequence, the specimens of Contracæcum from the black bass and the rock bass are herein designated as *Contracæcum brachyurum* (Ward and Magath, 1917).

Though the majority of the species ascribed to Contracæcum reach maturity in fish-eating birds and mammals and pass only the immature stages in the bodies of fishes, the present material includes fully mature worms bearing eggs. Walton (1928:65) has recorded the occurrence of Contracæcum from a number of fish hosts, one of which is the black bass. These individuals, from the Leidy Collections, were immature forms, encysted in the omentum of the fish. Walton interpreted these immature worms as belonging to *C. spiculigerum,* a form which reaches the adult state in pelicans, cormorants, and water turkeys. That Contracæcum is not an uncommon natural parasite of fishes is evidenced by the statement of Fujita (1932:36) who, in the introduction to a paper describing six new species from Japanese fishes, remarks that "Among parasitic nematodes, Contracæcum is one of the most prevalent forms that attack fish."

Contracaecum brachyurum (Ward and Magath, 1917)

Plate 38, Figures 4–6

Synonyms: *Hysterothylacium brachyurum* Ward and Magath, 1917; *Hysterothylacium cayugensis* (?) Wigdor, 1918.

Hosts.—*Micropterus salmoides, Ambloplites rupestris;* in stomach and intestine.

A large, robust worm; females about 8 cm. to 9 cm. long and 1 mm. in diameter, males about 6 cm. long and 0.9 mm. in diameter. Lips large and prominent, with well developed interlabia. Nerve ring about 0.5 mm. posterior to tip. Esophagus 6 mm. to 7 mm. long, with a clearly defined ventriculus. There passes forward from the intestine a single cecum which nearly reaches the anterior tip, 5.60 mm. in length. The esophageal diverticulum passes back from the ventriculus a length of about 1.0 mm.

Spicules equal, about 0.84 mm. in length. Arrangement of the male caudal papillæ cannot be discerned. Vulva some distance anterior to middle of body. Narrow lateral fins or alæ are present in the anterior region.

The eggs, viewed *in utero,* appear to be 0.060 mm. x 0.050 mm. Ward and Magath (1917) refer to a single cecum 0.94 mm. long, passing back from the esophageal ventriculus. Crediting this account the species has been removed to the genus Raphidascaris by later authors, where it belongs if the original account is correct.

Wigdor, 1918, described *Hysterothylacium cayugensis* from *Esox lucius* and *Ameiurus nebulosus* taken in Cayuga Lake. These specimens were all females and appear to agree closely with Ward and Magath's description. The same discrepancy arises, however, in that no mention is made of the anterior cecum.

Wigdor's material was only 20 mm. in length. If our assumption as to the identity of this material is correct the worms must have been very young and immature. Points of uncertainty arise in that Wigdor gives the impression that his material is mature; and furthermore, it occurs in the wrong host. Nevertheless his figure showing the esophageal cecum, lateral alæ and head region is so similar to Ward and Magath's figure of *H. brachyurum* and to our own material, that the weight of evidence is in favor of identity.

H. cayugensis is poorly figured and described, and in all probability is immature material of *Contracæcum brachyurum.*

While it appears necessary to take the above steps in order to clear the ground, it must be added that further study of this genus in fishes is badly needed. It is very probable that such study will reveal the presence of several distinct species from fishes in North America. But the existing descriptions are inadequate for any such separation as yet.

Biology of Contracaecum in Oneida Lake.—About one-half of the large-mouth bass examined carried this worm. The infested fish were taken from typical shoreline habitats around the west end of the lake. Infested rock bass were taken from similar shoreline localities. The open water rock bass do not appear to be infested. The worm seems to be more common in the black bass than in the rock bass and the former is probably its natural host. The life history is unknown.

Pratt had collected this species from the rock bass in his earlier survey, although he did not mention it in his report. His vial No. 2504 was found to contain specimens identical with our own material.

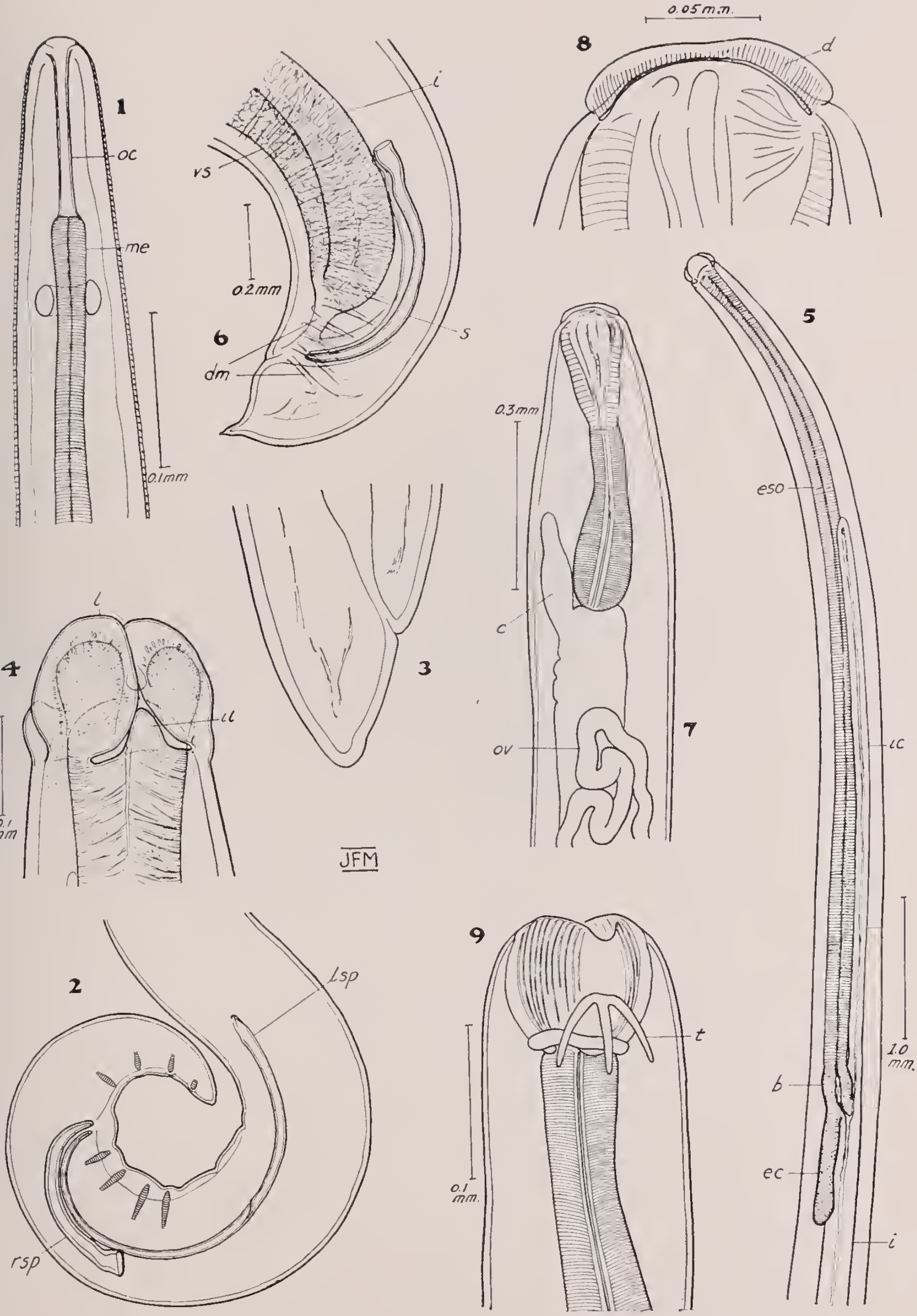
Nematoda: Order Spiruroidea

Definition: Usually more or less filiform worms; mouth usually with two lips. A chitinous vestibule may or may not be present behind the opening of the mouth. Esophagus usually long, cylindrical, and divided into anterior muscular and posterior glandular portions. Male: spicules usually unequal and dissimilar. Female: vulva usually near center of body.

Plate 38. Various nematodes. (Scale with Fig. 1 applies to Figs. 1–3.) 1, *Cystidicoloides harwoodi,* anterior end. 2, Tail of male. 3, Tail of female. 4, *Contracaecum brachyurum,* detail of head. 5, Anterior end showing esophagus and ceca. 6, Tail of male. 7, *Dichelyne cotylophora,* head region. 8, Detail of mouth, lateral view, showing cuticular lips with tooth-like markings, ventral surface on right. 9, *Camallanus oxycephalus,* head of immature specimen from the perch.

b—bulb, c—intestinal cecum, d—tooth-like markings, dm—diagonal muscles, ec—esophageal cecum, ic—intestinal cecum, me—muscular esophagus, oc—oral capsule, t—trident, vs—seminal vesicle.

Plate 38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The Spiruroidea is a large group, comprising numerous families, but only four of these are represented in our collections. These will be described in order.

Family Spiruridae

Definition: Spiruroidea: mouth usually with tri-lobed lateral lips, occasionally small dorsal and ventral lips may also be present, or lips absent. Usually a cylindrical chitinized vestibule. Esophagus long and cylindrical, divided into a short anterior muscular portion and a longer glandular part. Male: caudal alæ well developed and supported by pedunculated papillæ, of which there are almost always four preanal pairs. Female: vulva usually near the middle of the body; oviparous.

The family Spiruridæ is represented in our collections by worms of the genera Spinitectus and Cystidicoloides. Various authors have shown uncertainty as to the position of Spinitectus, the older of these genera, while Cystidicoloides has been but recently separated from Cystidicola by Skinker (1931). Yorke and Maplestone (1925) place Spinitectus under the Rictulariidæ, to which family it bears only a superficial resemblance in the possession of cuticular spines. Baylis and Daubney (1926) place it under the Thelaziinæ, subfamily of the Spiruridæ. This is also an untenable arrangement. These genera undoubtedly belong in the Spiruridæ, but have no relationship to the Thelaziinæ.

Skinker (1931), in a redescription of *Cystidicola stigmatura,* follows the old custom of placing the genus under the Thelaziidæ. She further separates from the genus Cystidicola, those forms in which the pre-anal papillæ are not doubled, placing these in the new genus Cystidicoloides. In the new genus are included *Cystidicoloides fischeri* and *C. harwoodi.* In the old genus there remain *Cystidicola stigmatura, C. farionis,* and *C. serrata.* Chitwood (1932) offers an improvement in placing both Cystidicola and Spinitectus under the Spiruridæ, keeping the Thelaziidæ as a separate family; but he separates Spinitectus as an appendix to the family, and of the soundness of this we are doubtful.

We believe that Spinitectus, Cystidicoloides and Cystidicola belong in the family Spiruridæ, and recognize the Thelaziidæ as a separate family. We would further assign these genera to a place in the subfamily Spirurinæ, which is founded chiefly upon negative characters such as lack of specialized lip and vestibular structures.

Genus Cystidicoloides Skinker, 1931

Cystidicoloides is apparently a well founded genus and is represented in our collections by *C. harwoodi.* The genus Cystidicola occurs in the air bladders of salmonid fishes and has not been found in Oneida Lake.

Cystidicoloides harwoodi (Chandler, 1931)

Plate 38, Figures 1–3

Synonyms: *Cystidicola harwoodi* Chandler, 1931; *Metabronema canadense* Skinker, 1931.

Host.—*Salmo fario;* in intestine.

Large females 12 mm. to 15 mm. in length. Males smaller, not more than 7 mm. or 8 mm. Cuticula of anterior region bears very coarse transverse striations at intervals of about 0.005 mm. Posterior edge of these striations sharp, tooth-like. Mouth leads into a tubular oral vestibule with thin cuticular walls. Esophagus begins about 0.120 mm. posterior to the tip. Nerve ring surrounds esophagus about 0.06 mm. back from its tip. Entire length of esophagus into body length about three times. Anterior muscular esophagus constitutes about one-fourth of the organ. Vulva near center of body, length anterior to that posterior as 5:4. Vagina approaches pore from rear, about 0.16 mm. long, branching into the bicornuate uterus. Ovejector present. Eggs 0.044 mm. x 0.028 mm. Tail of female blunt, almost round, anus near its tip.

Male shares general anatomical features of female. Tail falls into several coils. Moderate alæ present, anus rather near the tip. Papillæ, 4 pre-anal, and 5 post-anal, on either side. Some tendency, not very pronounced, for the papillæ to fall in pairs, not to be confused with the "double" papillæ of such species as *Cystidicola stigmatura* in which the two papillæ are in actual contact. Papillæ stalked, with slender bases and slightly bulbous extremities. Usually the first and last pre-anal are missing. Right spicule short and arcuate, with no barb, pointed at the pore and expands proximally; however, near its base it has a sudden constriction. Long left spicule slender. Proximally tubular, but about 1.3 mm. from its base it becomes suddenly compressed and curved into a trough or gutter. No cuticular cleats are present on the ventral surface of the tail.

Chandler's material, on which the species was named, came from the brook trout taken near Elizabethtown, N. Y. Our material extends the recorded host list to the brown trout. Infested specimens were fingerlings, taken from pools in Black Creek about one mile above its entrance into the lake. Mature trout in the lake and mill pond did not harbor the worm.

Skinker (1931) described *Metabronema canadense* from *Salvelinus fontinalis* from Quebec. This material has been compared with the type material of *Cystidicola harwoodi* described by Chandler from *Salvelinus fontinalis* from New York State, and the two are identical, *M. canadense* being merely a number of small specimens of the same species.

There appears to be some probability that Cystidicoloides, Skinker 1931, is synonymous with Metabronema, Yorke and Maplestone 1926, and that both of these are synonymous with Ascarophis, Van Beneden 1871. We have not had opportunity of studying original material to make certain of this point, but if such is the case the proper name for the genus is Ascarophis, by priority, and Cystidicoloides and Metabronema are synonyms.

The Genus Cystidicola Fischer, 1798

The genus Cystidicola is not very closely related to Cystidicoloides. The relationship between Cystidicoloides and Spinitectus is probably nearer.

Cystidicola stigmatura (Leidy, 1886) has been redescribed by Skinker (1931). This form is reported from the swim bladder of numerous fishes, chiefly salmonids. The species differs from *Cystidicoloides harwoodi* in possessing 5 to 9 pairs of pre-anal *double* papillæ, and in having the eggs provided with polar filaments, lacking in *C. harwoodi*. We did not find Cystidicola in Oneida Lake, although we made a careful search for it.

Genus Spinitectus Fourment, 1883

Definition: Like Cystidicoloides, but cuticula provided with rings of backwardly directed spines; rings at short intervals on anterior portion but more widely separated, and spines reduced posteriorly.

Because of undue emphasis upon the cuticular spines, an essentially superficial character, the true position of Spinitectus in the system has been misunderstood. Ignoring the cuticular ornamentation and considering fundamental anatomy the genus stands so close to Cystidicoloides that one could almost justify synonymizing the two. These fundamental similarities are found in the general shape, size and habitat of the worms, the character of the oral capsule, and esophagus; the female reproductive system, character of eggs; tail of male, and character of spicules and papillæ.

We have in our collections two species of Spinitectus, *S. gracilis* and *S. carolini,* the only species described from fresh-water fishes of North America. These species, which had hitherto been very inadequately known, were redescribed in detail in Part II of the present study.

Spinitectus carolini Holl, 1928

Hosts.—*Ambloplites rupestris, Eupomotis gibbosus, Micropterus dolomieu;* in intestine.

This form is remarkably similar in fundamental anatomy to *Cystidicoloides harwoodi.* The esophagus is equal to about one-third the length of the body. The muscular esophagus forms about one-fifth or one-sixth of the organ. The mouth capsule is cylindrical, about 0.10 mm. long. The vagina approaches the vulva from the rear and is 0.280 mm. long. The vulva is posterior to the middle of the body. Eggs are 0.036 mm. x 0.023 mm. The tail of the male possesses only narrow alæ, with four pairs pre-anal and five pairs post-anal papillæ. The spicules are as in *Cystidicoloides harwoodi,* but the short (right) spicule possesses a barb at the point. Cuticular cleats are present.

In all of the above fundamental points, agreement between *C. harwoodi* and *S. carolini* is so close that the situation is more like a comparison of two congeneric species, rather than members of separate genera. Actually the differences are more marked between *S. carolini* and *S. gracilis.*

Spinitectus gracilis Ward and Magath, 1917

Hosts.—*Esox niger, Lota maculosa, Ameiurus nebulosus, Pomoxis sparoides, Esox lucius, Leucichthys artedi tullibee,* and less commonly in *Ambloplites rupestris, Eupomotis gibbosus,* and *Salmo fario;* in intestine.

The reader is referred to Part II for a complete description of this species. It may be safely recognized by the following characters: male spicules, the short (right) member being bent twice with a terminal, lateral barb, and the longer spicule being tubular throughout its length; the male papillæ, four pre-anal, five post-anal on either side, on long slender stalks and all but the last grouped in pairs; the very short, crumpled, buccal capsule; the short esophagus—only one-ninth or one-tenth the body length; the much longer vagina, 0.8 mm. in length, which approaches the pore from the front; the size of eggs: 0.040 mm. x 0.024 mm.

For comparison these facts are set down in the following convenient form.

TABLE NO. 1. COMPARISON OF SPECIES OF SPIRURIDAE FOUND IN ONEIDA LAKE FISHES.

	C. harwoodi	*S. carolini*	*S. gracilis*
Length, mature females	12 mm.–15 mm.	7 mm.–8 mm.	10 mm.–15 mm.
Size of eggs	0.044 mm. x 0.028 mm.	0.036 mm. x 0.023 mm.	0.040 mm. x 0.024 mm.
Length of capsule	0.120 mm	0.10 mm	0.025 mm.
Vagina approaches pore from	Posterior	Posterior	Anterior
Length of vagina	0.16 mm.	0.28 mm.	0.8 mm.
Esophagus into body length	3 times	3 or 4 times	9 or 10 times
Muscular to glandular esophagus	1:2	1:5	1:3
Short spicule	Arcuate	Arcuate	Bent twice
Long spicule	Distal half compressed	Distal half compressed	Tubular throughout
Cuticular spines	Absent	Present	Present

Biology of Cystidicoloides and Spinitectus in Oneida Lake.—We have collected *C. harwoodi* but once, from three brown trout, 7 to 8½ inches long, taken in Black Creek about one mile above its entrance into Oneida Lake. Since we have never taken it in the lake this species is probably limited to streams. Black Creek is a trout stream with clear cold water, gravel bottom, sandy pools, and rapids. Neither of the two species of Spinitectus was found in these fish.

TABLE NO. 2. HOSTS CARRYING MATURE SPINITECTUS

(* denotes infestation)

Hosts	*Spinitectus carolini*	*Spinitectus gracilis*
A. rupestris	*	* (occasionally)
E. gibbosus	*	* (occasionally)
M. dolomieu	*	—
P. sparoides	—	*
A. nebulosus	—	*
L. maculosa	—	*
L. artedi tullibee	—	*
E. niger	—	*
E. lucius	—	*
S. fario	—	* (occasionally)

Spinitectus gracilis and *S. carolini* are found in the lake. *S. gracilis* has the wider range of hosts. *S. carolini,* on the other hand, is evidently limited. Most of these hosts contain only the one or the other species, but several fish contain both. The rock bass may simultaneously carry both *S. carolini* and *S. gracilis,* the former being more abundant in this host. The sunfish (*Eupomotis gibbosus*) likewise carries both species, often simultaneously, and again *S. carolini* is the more abundant. The brown trout carries both *S. gracilis* and *C. harwoodi,* but never simultaneously. The stream-inhabiting younger brown trout have *C. harwoodi* exclusively, whereas the older lake-inhabiting brown trout have *S. gracilis* and never *C. harwoodi.* Apparently the trout is not a favorable host for *S. gracilis,* which seldom matures in this fish.

Cystidicoloides harwoodi must be regarded as restricted to the young stream-inhabiting brown trout. It does not occur in the warmer sluggish water, often with mud bottom, in which the old trout frequently take up their residence. Thus we do not find it in brown trout from the mill pond at Cleveland (a wide muddy expansion of Black Creek, a trout stream), or in Oneida Lake.

Spinitectus gracilis is found more abundantly in *Esox niger* and *Lota maculosa.* In both these fishes its incidence is very high and it reaches maturity with great frequency. Both fishes are of the mud-bottom type, but the ling is a deep-water fish, whereas the pickerel is restricted to shallow water near shore. The remaining hosts of *Spinitectus gracilis* all prefer mud bottom, but are found at different levels in the lake, from the deepest part up to the shore line. It therefore seems probable that *S. gracilis* is linked up with mud bottom, but independent of depth.

Spinitectus carolini occurs with greatest frequency in the sunfish. It is also not uncommon in the rock bass, but the sunfish is probably the normal host. Both these fishes are more or less restricted to shallow water, although they frequent both soft and hard bottom. Since we have never taken this parasite from a fish from deep water, it seems probable that the species is limited to the shallow-water areas, but is apparently indifferent to the type of bottom. The species is not so abundant as *S. gracilis.*

A contrast may thus be drawn between the three species of the group, as follows. *Cystidicoloides harwoodi* occurs in tributary trout streams, never in the lake. *Spinitectus carolini* and *S. gracilis* occur in the lake, or in sluggish water, but not in trout streams. Of the two lake species one is correlated with shallow water independent of bottom (*S. carolini*). The other is correlated with mud bottom independent of depth (*S. gracilis.*).

Perca flavescens, and *Stizostedion vitreum* carry immature Spinitectus in abundance. In addition, *Cyprinus carpio, Notemigonus crysoleucas, Ameiurus natalis, Noturus flavus,* and *Percopsis omisco-maycus* have been found to contain immature Spinitectus in very small numbers. That the worms never attain maturity in these fishes proves that they are incapable of serving as hosts.

There is an almost total absence of infestation in the large basses. We have but a single record of mature worms from the small-mouth bass, and likewise a single record of immature worms from the large-mouth bass. It would seem that the feeding habits of these fishes prevent them from becoming infested, as otherwise the worms would be found more frequently, even if, as in the perch, they were immature and unable to complete their development.

Appendix to Spirurinae

The genus Rhabdochona is little understood, but it appears to belong somewhere near the preceding species. Chitwood (1932:168), on the basis of head characters viewed *en-face,* regards it as a doubtful member of the Thelaziidæ. On the general anatomical characters available from the work of previous authors, we are inclined to treat this genus in the same fashion as Spinitectus and Cystidicola and remove it from the Thelaziidæ to the Spiruridæ, subfamily Spirurinæ. It appears to agree with Spinitectus and Cystidicola in the spicules, arrangement of papillæ on the tail of the male, relation of vagina and uteri and other features.

A single species, *Rhabdochona cascadilla,* has been reported from this continent by Wigdor (1918). The species occurred in minnows in Cascadilla Creek, tributary to Cayuga Lake, N. Y. We have not found this genus in Oneida Lake.

Family Hedruridae

The Hedruridæ comprise a single genus, the members of which are found most frequently in the digestive tract of reptiles and amphibians. Chandler (1919) and Walton (1930) have recorded species from North American Amphibia, while the present writers described *H. tiara* in Part I of this survey. This is the first record of a member of this genus from the fresh-water fishes of North America.

Genus Hedruris Nitzsch, 1821

Definition: Mouth with four lips, the two lateral smaller and with elaborately lobed and curved edges. The median large, thin, and triangular, their broad bases almost covering the lateral lips. Eight cone-shaped cuticular swellings behind lips. Short vestibule present; esophagus having at its anterior end a sculptured chitinous ring. Tail of female invaginated to form a deep sucker, provided with a large chitinous hook. Vulva near anus.

Hedruris tiara Van Cleave and Mueller, 1932

Hosts.—*Esox niger* and *Erimyzon sucetta oblongus.* In stomach.

Taken only twice, each time but a single specimen being found. Described as new in Part I. No new material has come to hand.

Family Camallanidae

Definition: Mouth elongate dorso-ventrally and buccal capsule usually consisting of two shell-like chitinous valves. Esophagus divided into muscular and glandular portions. Male with caudal alæ, stalked papillæ, and unequal, dissimilar spicules. Female with vulva near middle of body, vagina directed posteriorly, uteri opposed, posterior limb ending blindly without an ovary. Viviparous.

Represented in our collections by a single genus.

Genus Camallanus Railliet and Henry, 1915

Definition: Buccal valves furnished with parallel longitudinal ribs on inner surface. A trident-shaped chitinous process at junction of valves with points directed caudad. A circular collar at junction of capsule and esophagus, and no secondary buccal capsule. Attachment to the tissues of the host intestine is attained by clamp-like action of the powerful lateral jaws.

Two species of this genus have been recognized for the North American fresh-water fishes. Both of these were described by Ward and Magath (1917), and are differentiated by Ward (1918), in *Fresh-water Biology,* as follows:

Key to the Species of Camallanus From Fresh-water Fishes of North America

(An asterisk (*) indicates species found in the Oneida Lake fauna.)

1 (a) Anterior end bent ventrad with buccal capsule set at an angle to the body axis .... **C. ancylodirus**

(b) Anterior end attenuated, not bent .... **C. oxycephalus***

Camallanus oxycephalus Ward and Magath, 1917

Plate 38, Figure 9

Host.—*Ambloplites rupestris,* immature specimens in *Perca flavescens;* in intestine.

Ward and Magath (1917) described two species of this genus: *C. ancylodirus* from the German carp, and *C. oxycephalus* from the white bass and black crappie at Fairport, Iowa.

The genus seems rare in Oneida Lake. Our material consists of two minute, post-larval specimens from the perch, and two large worms from the rock bass. These last were collected by Pratt in his original survey of Oneida Lake parasites, but at this date they have blackened so badly that their internal anatomy cannot be discerned. They were identified originally by Pratt (1923:63) as *C. oxycephalus.* We have never taken the adult worms in our own work.

Pearse (1924a:177) has commented upon the frequency with which this nematode protrudes from the anus of the host. The species is apparently susceptible to post-mortem changes within the host and migrates following the death of the fish.

Family Cucullanidae

Definition: Head provided with lateral lips, each bearing three papillæ. Mouth vertical, slit like; esophagus muscular throughout with posterior club-shaped swelling, and dilating anteriorly into a pseudo-buccal cavity. Intestine simple or with cecum. Male: Pre-anal sucker present or absent; spicules equal or unequal; gubernaculum usually present. Female: Caudal extremity terminating conically and fairly abruptly. Vulva near middle of body, vagina directed anteriorly, with two ovaries. Oviparous.

Törnquist (1931) divides the family into four genera as follows:

Group A. Without intestinal cecum

1. Cucullanus, Mueller, 1777. With mouth at right angles to long axis of body (i.e., front end square with body); mouth laterally compressed, with armament of cuticular ridges. No cuticular ridges along side.

2. Dacnitis, Dujardin, 1845. With mouth oblique to long axis of body, (i.e., ventral angle projects farther forward than dorsal angle). No specialized oral armature. Mouth cavity fairly rounded. Lateral longitudinal ridges present.

Group B. With cecum

3. Cucullanellus, Törnquist, 1931. With ventral cecum; small worms, with a pronouncedly spindle-shaped body and powerful sucker.

4. Dichelyne, Jägerskiöld, 1902. With a dorsal cecum, and of fairly even diameter throughout.

Genus Dichelyne Jägerskiöld, 1902

Synonym: Dacnitoides, Ward and Magath, 1917.

This genus is composed of several species parasitic in fishes. The first to be described, and type of the genus, is *D. fossor* Jägerskiöld, 1902. Ward and

Magath, 1917, erected the genus Dacnitoides for the species *D. cotylophora* which differs from Dichelyne only in the alleged fact that one ovary was supposed to be present in Dacnitoides. In other characters the genus agrees with Dichelyne. Törnquist restudied material of this species and recognized Dacnitoides as a synonym of Dichelyne. He found an agreement in all characters, except the supposed absence of the posterior ovary, with conditions found in the genus Dichelyne. He was unable to settle the point in regard to the ovary because of inadequate material, but he expressed doubt concerning the absence of the second ovary. Mueller (1933) has determined that both ovaries are present, thus confirming Törnquist's conclusions regarding the synonymy.

Dichelyne cotylophora (Ward and Magath, 1917)

Plate 38, Figures 7–8

Hosts.—*Perca flavescens, Stizostedion vitreum, Micropterus salmoides, M. dolomieu, Ambloplites rupestris, Ameiurus nebulosus, Leucosomus corporalis.* In intestine.

Females about 5 mm. long, and males slightly shorter. Body straight in female. Male tail flexed ventrally into a hook. Esophagus divided into two parts, with the line of separation marked by a slight constriction, and with expanded extremities. A true capsule lacking, since the esophagus is in direct contact with the lips. Mouth a vertical slit. Lips provided with a cuticular margin which projects anteriorly and has fine tooth-like markings along its base. Four papillæ on the anterior surface of the head.

The vulva lies behind the center of the body, about one-third the body length from the tail. The vagina passes anteriad, and branches into the bicornuate uterus about 0.4 mm. inside the pore. In numerous cases we are able to see in our material a completely symmetrical female reproductive system, with the two branches of the uterus leading into two separate ovaries, and we are able to trace these ovaries to their respective apical cells. One ovary is usually coiled in the anterior region of the body just posterior to the esophagus. Its end usually is bent backward for a short distance in front of the apical cell. The other ovary is found in the posterior part of the body. Its terminal filament projects directly backward and its apical cell lies near the caudal extremity. The uteri are short, thin-walled, and contain a relatively small number of large, thin-shelled eggs. The eggs are about 0.064 mm. by 0.040 mm. in diameter. The females of this species can be distinguished from those of the following in that usually the ovarian coils are entirely posterior to the esophagus in *cotylophora*, while in *robusta*, the ovarian coils usually lie alongside the esophagus, extending well forward into the head region.

The male of *Dichelyne cotylophora* has the general anatomical characters of the female. However, a large ventral sucker is present a short distance anterior to the cloacal aperture. Papillar formula somewhat complicated, five papillæ on each side anterior to the cloaca. One pair on the anterior border of the sucker, the remaining four pairs posterior. A small ventral median papilla on the anterior lip of the anus. Posterior to anus, six papillæ on each side. First, third, fourth and sixth pairs of post-anal papillæ ventro-lateral, in line with those anterior to anus. Second and fifth pairs dorso-lateral. Fourth and fifth pairs of diminutive size, rarely the fourth post-anal papilla may be double. Total number of papillæ present 23; 11 pre-anal, 12 post-anal.

Spicules equal, long, ribbon-like, when withdrawn extend within the body about as far in front of the sucker as the distance from the sucker to the pore. They are about one-sixth the total body length, their ends pointed and crinkled. When exserted, the spicule flattens out into a wide band; when withdrawn, it necessarily curls edgewise to accommodate to the available space. Gubernaculum present.

This species is by far the commonest form of Dichelyne in Oneida Lake, *Perca flavescens* is its chief host. The incidence of infestation in the adult perch is high—about 60 per cent. Seventy fingerling perch examined did not harbor the parasite. In the other hosts infestation is only occasional and light. Often 10 or 15 worms are found in a single perch; seldom any more, and frequently as few as 2 or 3. We find infested perch from nearly all localities where we have taken this host: Shepherd's Point, Fairchild Bay, Johnson's Bay, Walnut Point, Poddygut Bay, Short Point Bay, Lower South Bay, Old Man Bay, Dunham Island, Lakeport Bay, Jennings Point, 50-foot depth off Cleveland, 30-foot depth off Shackleton Shoals, 20-foot depth off Cleveland. The parasite evidently continues its activities in the perch uninterruptedly during the year. Most of our records are for the summer months from May to September, but we also have records for infested perch taken through the ice in December and January.

Dichelyne robusta (Van Cleave and Mueller, 1932)

Hosts.—*Ameiurus nebulosus, A. natalis.* In intestine.

Described by us in Part I of this series. Tail of male hooked, as in *D. cotylophora,* but sucker lacking. Spicules ribbon-like, not more than half as long as in *D. cotylophora,* and when withdrawn not passing the anterior pair of papillæ. Gubernaculum present. Papillæ much as in *cotylophora.* Pratt (1923) reported from *Ameiurus natalis* of Oneida Lake, "a few small nematodes about 5 mm. long belonging to the genus Cucullanus." On re-examination this material proves to be *Dichelyne robusta.*

This worm is comparatively uncommon and is limited in its host relationships to silurids. We have taken it from only *Ameiurus nebulosus* and *A. natalis.* It is apparently more abundant in *A. nebulosus.* None of the other species of Siluridæ examined by us has harbored the worms. In its chief host it is not very common, its incidence being not above 10 per cent. Likewise intensity of infestation is low. We have usually found only two or three worms in a single host. The infested bullheads came from various shallow-water localities, *A. nebulosus* from Fairchild Bay, Short Point Bay, small tributary of Chittenango Creek near Bridgeport, and the harbor of Cleveland. *A. natalis* came from the vicinity of Cleveland.

Appendix to the Cucullanidae

Genus Haplonema Ward and Magath, 1917

The genus Haplonema was erected by Ward and Magath, 1917, for a species of nematode parasitic in the fresh-water dogfish, Amia. They note the very generalized character of the genus, the necessity of defining it chiefly in negative characters, and the difficulty of locating it in the system. Yorke and Maplestone (1926) place it as the last genus under the Thelaziidæ, but it does not fit clearly into this family, being the only included genus with equal spicules, and standing close to such obviously unrelated genera as Cystidicola and the little understood Rhabdochona. Baylis and Daubney (1926) isolate the genus Haplonema as an appendix to the Filarioidea.

The following description is modified from Ward and Magath.

Diagnosis: Body rather robust, but not large; anterior end bent or coiled, without lips, but with lateral alæ ("wings"). No buccal capsule; esophagus muscular, without bulb, divided into two regions by partition near center. Posterior end of female straight or slightly curved behind anus. Posterior end of male without bursa or alæ, with two equal spicules of moderate length. Ovary laid in transverse loops ventral to intestine in both anterior and posterior regions. Uterus with anterior and posterior branches, vulva near center of body. Oviparous.

At the time the genus Haplonema was founded (1917) it was represented by a single species, *H. immutatum*. More recently Moulton (1931:105) has recognized a second species parasitic in *Lota maculosa* and to it has applied the name *H. hamulatum*. Specimens from eels in Oneida Lake belong to this genus, but do not agree with the characters of either of the preceding species.

Haplonema sp.

Plate 39, Figures 1–4

Host.—*Anguilla rostrata*, in intestine.

This form is evidently new, and although figured in the plates is not named here. For a description of this species see Part IV.

Systematic Position of Haplonema

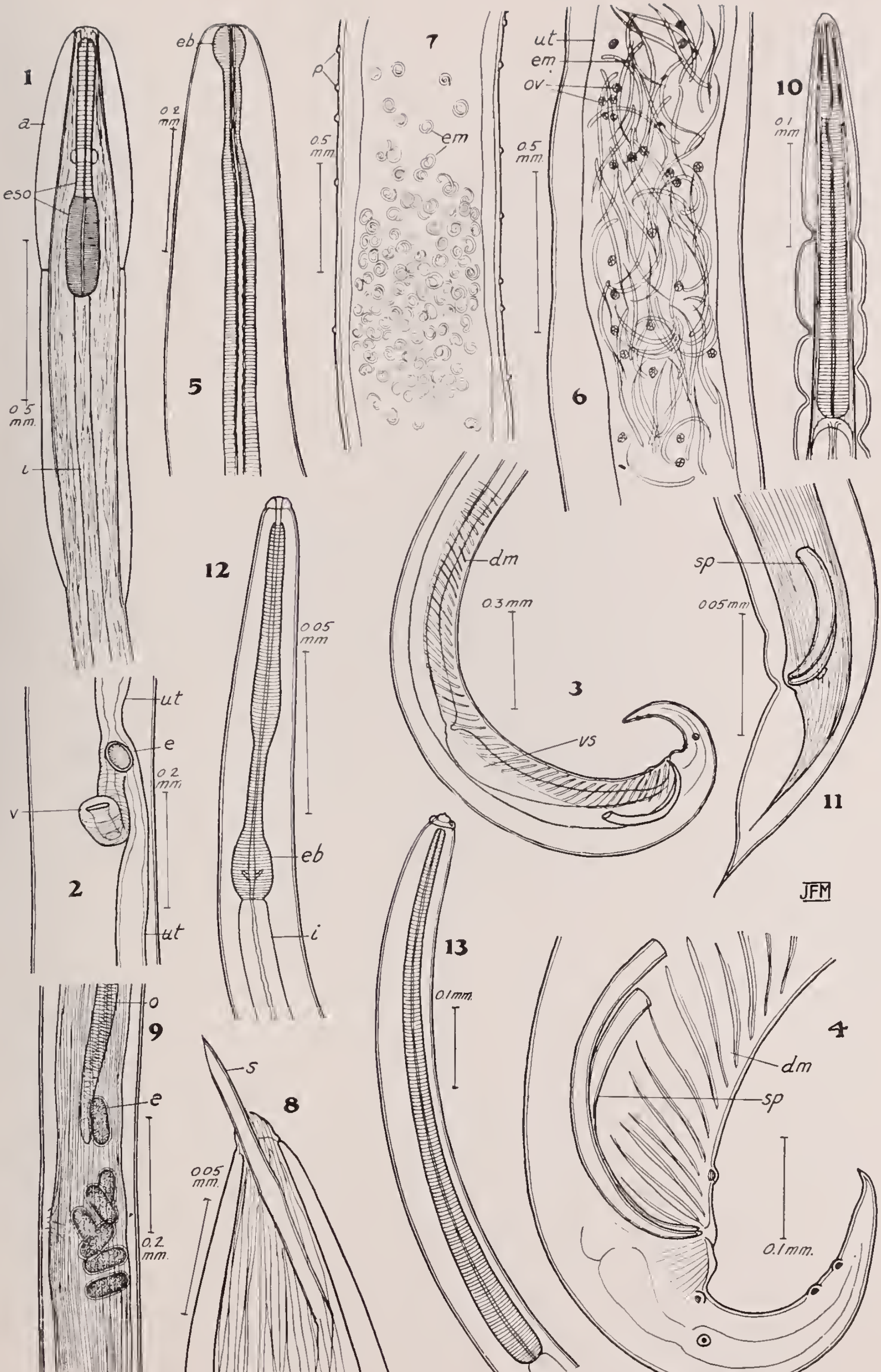
It seems obvious that Haplonema does not belong with any of the groups to which it has hitherto been assigned. It differs from the Thelaziidæ in possessing equal spicules, and in lacking a buccal capsule. The other members of the family are found in the orbital, nasal or oral cavities of mammals and birds or in the air sacs of birds.

It seems more probable that Haplonema belongs with the Cucullanidæ. It fits into this family on the general character of the esophagus and the absence of an oral capsule. Its anatomy is more simplified than that in other genera of the family but conforms to their fundamental type. The general character of the tail of the male, with its long series of diagonal muscles, ribbon-like spicules, and the general shape and plan of the papillæ, conforms to the conditions in Dichelyne. The alæ of the head may be cited as a divergent character, but these are superficial structures. A further general consideration in favor of the transfer of the genus to the Cucullanidæ is the fact that all members of this family occur in the intestine of fishes.

Plate 39. Various nematodes. 1, *Haplonema* sp., head region. 2, Mid region of female. 3, Tail of male. 4, Detail of tail of male, showing papillae. 5, *Philometra cylindracea*, head of specimen taken from perch in winter. 6, *P. cylindracea*, mid region of mature female. 7, *P. nodulosa*, mid region of mature female. 8, *Dorylaimus* sp., head end, from Erimyzon. 9, *Dorylaimus* sp., mid region of female, from carp. 10, Nematode, type 1, (Monhystera?) anterior end. 11, Nematode, type 1, (Monhystera?) tail of male. 12, Nematode, type 2, (Cephalobus?) head region. 13, Nematode, type 3, head region.

a—alae, dm—diagonal muscle of tail, e—egg, eb—esophageal bulb, em—embryos, eso—esophagus, i—intestine, o—ovary, ov—developing ova, p—cuticular papillae, s—spear, sp—spicules, ut—uterus, v—vulva, vs—seminal vesicle.

Plate 39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Nematoda: Order Filarioidea

Definition: Filiform worms; mouth usually simple and without lips; buccal capsule absent or rudimentary; esophagus divided into two parts. Intestine sometimes atrophied posteriorly. Male: Spicules usually very unequal and dissimilar. Female: Almost always much longer than male; vulva usually in esophageal region. Parasites of circulatory, lymphatic, muscular, or connective tissues, or of serous cavities, of vertebrates.

Two families are distinguished as follows: Filariidæ: Females at most three or four times as long as males; vulva not atrophied in gravid female.

Dracunculidæ: Females much larger than males, vulva atrophied in gravid female. (Represented in our collection by two species of Philometra—one of the two genera in this family.)

Genus Philometra Costa, 1846

Definition: Female very much larger than male; body filiform; anterior and posterior extremities rounded; mouth with or without lips and head papillæ; esophagus cylindrical and very short. Male: Posterior extremity rounded, cloaca terminal, bordered by two lips; spicules equal and needle-like; gubernaculum present. Female: Anus and vulva atrophied; vulva in young worms at the junction of the middle and posterior thirds of body; body occupied almost entirely by embryo-filled uterus. Small ovary at each end of body. Parasitic in the body cavities and tissues of fishes.

Philometra cylindracea (Ward and Magath, 1917)

Plate 39, Figures 5–6

Synonym.—*Ichthyonema cylindraceum* Ward and Magath, 1917.

Host.—*Perca flavescens,* in body cavity.

The following is taken from the original description of Ward and Magath (1917:63). "Male unknown, probably minute. Mature female 100 mm. long, of nearly equal diameter (0.48 mm.) everywhere. No lips or papillæ. Esophagus 1.09 mm. long, 0.066 mm. in diameter. Vulva and vagina atrophied, no vestiges discernible. Uterus crowded with undeveloped ova (i. e., female unimpregnated), ova almost spherical, measure 0.044 mm. in diameter." They further add: "In Europe almost half of the females found are like our material, unimpregnated owing apparently to a scarcity of males."

Our material is assignable to this species. However, our worms were larger and measured as much as a foot in length. All were crowded with living embryos. The worm in life has a reddish color and is extremely delicate. No males were found. Three of our collections were made from a total of 36 perch collected July 16, 17, and 24, from deep water off Cleveland. In several cases, the worms were found atrophied, and living embryos had escaped in masses into the body cavity of the fish, around the region of the bladder. In examining four perch from Big Bay, February 28, 1931, a fragment of this worm was found showing the occurrence of this infestation in the winter months.

Although this worm is not uncommon in Oneida Lake, it seems limited to the deep-water perch and in these its incidence is probably less than 5 per cent. Usually only one worm is found in a fish, but on one occasion three were taken from a single perch, one worm occurring in the pericardial cavity.

Philometra nodulosa Thomas, 1928

Plate 39, Figure 7

Host.—*Catostomus commersonnii,* in galleries in connective tissue of lips and cheek.

Represented in our collection by a fragment dissected from the cheek of a common sucker found in the collections of the Roosevelt Station. The fish was taken in Butternut Creek, above Jamesville Reservoir, on June 11, 1928. This creek is a tributary of Oneida Lake. We did not find the species in Oneida Lake.

The following description is largely taken from Thomas (1928:193): Glistening white in living state, 28 mm. long by 0.456 mm. in diameter. Anterior end rounded, posterior tip truncated. Irregularly placed transverse bosses on cuticula from end to end forming a series of incomplete rings. Mouth terminal with six minute lips. Anterior portion of esophagus somewhat bulbous. Intestine degenerate and no trace of anus. Uterus packed with active larvæ.

The larvæ live only from one to three days unless eaten by a suitable copepod. Thomas found the larvæ capable of infesting *Cyclops brevispinosus.* No great increase in size took place within the body cavity of infested Cyclops. Accident cut short further experiments to transfer the infestation to the sucker as final host, so that the life history of this worm is still uncertain.

Miscellaneous Nematodes

Very minute free living or larval nematodes were encountered in various hosts during this survey, at times occurring free in the intestinal tract, at times encysted in various parts of the body. While in one case these worms are certainly larval, in others they appear to be free living forms which had been taken into the host by accident (pseudoparasites). We cannot identify them as to species, but in the following sections they are described and numbered according to type.

Type 1, Monhystera?

Plate 39, Figures 10–11

Host.—*Percopsis omisco-maycus.* In intestine.

We found only five of these worms. Length about 2.0 mm., width 0.060 mm. Cuticula loose and expanded away from the body, much like a sheath. Shape filiform, tapering at both ends to an acute point. Lips not apparent. Esophagus cylindrical, tapering, without posterior swelling or bulb, equal to one-eighth the body length. One specimen, a male, showing slight indication of a series of diagonal caudal muscles. Spicules equal, arcuate, blunt, and relatively heavy, 0.068 mm. long. Probably a free living species (Monhystera?).

Type 2, Cephalobus?

Plate 39, Figure 12

Host.—*Salmo fario.* In intestine.

Exceedingly small, 0.385 mm. in length, 0.024 mm. in width. Esophagus oxyuroid. Entire esophagus equal to about one-sixth body length. In some individuals (females?) what appears to be the rudiment of the gonad, in the form of a string of cells, lies near the middle of the body, with one end (the future pore?) attached to the cuticula just about the center. Further features of diagnostic value are not discernible. Probably a free living species.

Type 3, Larval nematode

Plate 39, Figure 13

Host.—*Notemigonus crysoleucas, Umbra limi, Perca flavescens;* encysted in wall of intestine. *Eupomotis gibbosus;* encysted in liver.

Yellow in life, 2.5 mm. to 3.0 mm. in length, and 0.08 mm. in diameter. Body cylindrical, blunt at anterior end, sharply conical at posterior end. Cuticula thin and tightly fitting. Mouth slit-like with lateral lips, each set with a small median elevation or tooth. A very slight, forwardly directed cuticular collar surrounds the edge of the head. Esophagus cylindrical, slightly more than one-fourth the length of the body and of the same structure throughout. We are unable to distinguish any sex differences in these larvæ, all having the same general anatomy suggestive of females. This worm is probably the young of a Spirurid.

Type 4, Dorylaimus sp.

Plate 39, Figures 8 and 9

Host.—*Erimyzon sucetta oblongus, Eupomotis gibbosus, Cyprinus carpio, Percopsis omisco-maycus.* In intestine.

In our work a species of nematode was encountered on several occasions which was at first thought to be a larval parasitic nematode, but has since been recognized as belonging to the genus Dorylaimus. This genus comprises numerous free-living species inhabiting soil and fresh water. Such worms could have entered the fish only accidentally along with mud, while the fish was rooting on the bottom.

This worm is about 4 mm. long and 0.165 mm. in diameter, spindle-shaped, evenly tapering to a fine point at both ends. The mouth is simple, without any trace of lips, and is provided with a spear 0.09 mm. long. The anus is very near the caudal tip. The female genital pore appears to lie near the anterior third of the body. Esophagus equal to about one-fourth the length of the body, cylindrical without terminal bulb or inflation. One specimen from the carp contains eggs measuring 0.100 mm. x 0.040 mm.

SECTION 5. TAXONOMY AND BIOLOGY OF THE ACANTHOCEPHALA OF ONEIDA LAKE FISHES

Acanthocephala.—The Acanthocephala or thorny-headed worms which occur in fishes, are elongate and flattened and become distended and practically cylindrical when placed in water or in a killing fluid. The sexes are separate and in each the anterior extremity of the body is provided with a specialized attachment organ called the proboscis. This proboscis is capable of inversion and retraction within the front end of the body. When everted, its surface bears numerous recurved hooks and spines which grapple into the host tissue and thereby provide secure attachment for the parasite. Like the tapeworms, these parasites have no trace of a digestive system, and the digested food of the host is absorbed directly through the body surface of the worm. Normally, the Acanthocephala live as adults in the lumen of the digestive tract only, but in relatively rare instances adult worms bore through the wall of the digestive tract and come to lie in the body cavity, or undergo encystment in the viscera. Immature worms may likewise be found encysted in any of the internal organs.

A total of four species of Acanthocephala are encountered in the fishes of Oneida Lake. These are, in the order of their abundance in our collection: *Neoechinorhynchus cylindratus* (Van Cleave), *Leptorhynchoides thecatus* (Linton), *Pomphorhynchus bulbocolli* Linkins and *Octospinifer macilentus* Van Cleave. To show the relative position of these in the entire list of acanthocephalans a key to the known genera infesting fresh-water fishes of North America is given here.

Key to the Genera of Acanthocephala Reported From Fresh-water Fishes of North America

(An asterisk (*) designates the genera found in Oneida Lake fishes.)

1 (a) Proboscis globular or pyriform, carrying but three circles of hooks. Cement gland of male always a single syncytial mass 2
(b) Proboscis not globular, carrying more than three circles of hooks. Cement gland of male a syncytium, or 4 or more separate glands 4
2 (a) Six hooks in each of the three circles .... **Neoechinorhynchus***
(b) More than six hooks in each circle 3
3 (a) Eight hooks in each circle .... **Octospinifer***
(b) Twelve hooks in each circle .... **Gracilisentis**
4 (a) Proboscis at the tip of a long, cylindrical neck with usually a globular expansion of the neck just posterior to the proboscis .... **Pomphorhynchus***
(b) Proboscis attached to the anterior end of body proper directly or at least without a long cylindrical neck between body and proboscis 5
5 (a) Cement gland of male a syncytial mass bearing sixteen giant nuclei ... **Tanaorhamphus**
(b) Several distinct cement glands posterior to testes of male 6
6 (a) Four cement glands .... **Fessisentis**
(b) More than four cement glands 7
7 (a) Lemnisci about the same length as proboscis receptacle. Proboscis hooks not surrounded by cuticular elevations .... **Echinorhynchus**
(b) Lemnisci much longer than proboscis receptacle. Proboscis hooks each surrounded by a cuticular collar .... **Leptorhynchoides***

The relatively small number of Acanthocephala here recorded does not mean that these worms are unimportant in the fishes of Oneida Lake. The embedded proboscis with its recurved hooks causes damage to the intestinal wall of the host and ulcer-like lesions and conspicuous areas of laceration and inflammation sometimes result. Pearse (1924:187) lists Acanthocephala among the most injurious parasites of fishes because of the apparent injury to the host tissues.

Little is known of the life cycle of the Acanthocephala of fishes. All members of this group are the most thoroughly adjusted to the parasitic habit of any of the parasitic worms. The dependent state has been so firmly impressed on all acanthocephalans that there is no time when the individual leads a free life even for a brief interval. In so far as known, every species utilizes at least two hosts, of which one is a vertebrate, in the digestive tract of which sexual maturity is attained, and the other is an arthropod which shelters the larva. Eggs produced by the mature worm leave the body of the vertebrate host along with the feces. Each egg contains an embryo which is wholly incapable of breaking its confining shells and never hatches unless it is swallowed by some suitable species of arthropod. Some kind of crustacean or insect acts as the first host, in every life history cycle which has been determined. In the simplest conditions, the larva inside the body of the arthropod host is liberated in the digestive tract of a fish which swallows the arthropod. Consequently there is no period when the acanthocephalan leads a free existence. The entire life cycle is intimately tied up with and conditioned by food chains and feeding habits. In some species additional links are joined into the life cycle. The arthropod host may transmit the immature larva to some vertebrate which is incapable of bringing it to maturity. In such an instance the larva has a chance for completing its development only in case the fish sheltering it is devoured by some other fish suitable for bringing the worm to the functional reproductive state. Mature acanthocephalans are never found normally in any organ outside the digestive tract. In this limitation of seat of infestation the Acanthocephala resemble the cestoda. The following descriptions are based upon preserved specimens.

Family Neoechinorhynchidae

The family Neoechinorhynchidae seems to be an old one with especially great diversification on the North American continent. With the exception of one species which lives in the digestive tract of fresh-water turtles, all the representatives of the family reach sexual maturity in fishes. Presence of a small number of ovoidal giant nuclei in the subcuticula and the lemnisci, and of a single large cement gland in the male, are characters possessed by all members of this family. The receptacle of the proboscis is always a simple sac, the wall of which is composed of a single layer of muscle.

Two of the genera found in the fishes of the Oneida Lake region belong to this family, and each is here represented by a single species. These are the widely distributed Neoechinorhynchus, holarctic in its range, and a peculiarly North American genus, Octospinifer.

Genus Neoechinorhynchus Hamann, 1905

As type of the family, this genus is characterized by the possession of a globular proboscis which bears three circles of six hooks each. The hooks of the terminal circle are heavy, strongly recurved, and each bears a distinctly enlarged, plate-like root within the tissue of the proboscis. The hooks of the remaining circles are considerably smaller and lack highly developed basal structures. Four species have been recognized in the fishes of this continent, but only one of these has been recorded from the eastern states, namely, the commonest representative of the genus, *N. cylindratus*.

Neoechinorhynchus cylindratus (Van Cleave, 1913)

Plate 40, Figures 1–3

Hosts.—*Micropterus salmoides, M. dolomieu, Ambloplites rupestris, Stizostedion vitreum, Esox niger, E. lucius, Amia calva, Erimyzon sucetta oblongus* and *Anguilla rostrata*; in intestine. Occasionally in intestine of numerous other fishes.

Specific Diagnosis.—Body large, almost cylindrical except in young forms in which the posterior region is gradually narrowed. With five giant nuclei in mid-dorsal line of body and one in mid-ventral line. Females 10 mm. to 15 mm. long, with a maximum diameter of about 0.7 mm. a short distance posterior to the proboscis. Males 4.5 mm. to 8.5 mm. long and 0.5 mm. to 0.7 mm. in diameter. Proboscis globular, slightly broader than long (0.172 mm. by 0.150 mm.). Proboscis hooks in three circles of six hooks each, in terminal circle 0.079 mm. to 0.097 mm. long, in middle circle 0.037 mm., in basal circle 0.021 mm. to 0.025 mm. Roots of first circle of hooks about 0.058 mm. long, and 0.029 mm. broad; those of second circle much smaller, while in third or basal circle the posteriorly directed roots are practically wanting. Embryos within gravid female usually 0.049 mm. to 0.051 mm. long, and 0.015 mm. to 0.021 mm. in diameter.

Van Cleave (1923:80) states that "*Stizostedion vitreum* is the most generally utilized host of *N. cylindratus* in Oneida Lake." Further data, available in the results of the present survey, give evidence that *Micropterus salmoides* is more frequently infested with *N. cylindratus* and carries much larger numbers of individuals per host than does Stizostedion. Several specimens of the large-mouth bass carried massive infestations of this worm. *N. cylindratus* is fairly evenly distributed in Oneida Lake. At the west end and along the south shore the large-mouth black bass is its most significant host; and along the north shore and at the east end, where the large-mouth black bass is less often found, the pike perch takes its place as chief host of this parasite.

Many species of fish could be listed as host of this parasite on the strength of one or a few instances of its occurrence. In a number of these hosts the adjustment is obviously imperfect, as indicated by the complete lack of gravid females.

The yellow perch frequently contains this parasite, but in the majority of cases only one or two individuals were present in each fish, and these were very often immature.

Genus Octospinifer Van Cleave, 1919

The genus Octospinifer was created to accommodate a single distinctive species of acanthocephalan which differs from all other known Neoechinorhynchidae in the possession of eight hooks in each of three circles around the globular proboscis.

To date, there has been but a single species assigned to this genus, *O. macilentus*, a description of which follows.

Octospinifer macilentus Van Cleave, 1919

Plate 40, Figures 4–5

Host.—*Catostomus commersonnii*, in intestine.

Specific Diagnosis.—Body long, approximately cylindrical, tapering slightly toward posterior extremity. Males about 4 mm. long, females about 10 mm.; maximum diameter about 0.4 mm., although in some gravid females it reaches 0.58 mm. Genital opening of female on ventral surface about 0.1 mm. from the posterior extremity of the body. Posterior extremity of body about 0.19 mm. in diameter. Proboscis short, globular, usually slightly broader than long; length about 0.106 mm., diameter about 0.120 mm. The eight hooks of terminal circle equal in size; not conspicuously larger than hooks of remaining circles. Terminal hooks 0.041 mm. long; hooks of middle circle 0.032 mm. to 0.035 mm.; those of basal circle 0.024 mm. to 0.030 mm. Testes elliptical, not crowded together. Sperm ducts of mature males frequently showing a number of vesicular enlargements between the posterior margin of the anterior testis and the anterior margin of the cement gland. Cement gland not in close contact with posterior testis, frequently broadly separated from it; form typical of the family, containing eight giant nuclei. Embryos within body cavity of mature females, 0.030 mm. to 0.047 mm. long, by 0.015 mm. to 0.018 mm. wide.

O. macilentus is one of the commonest parasites of young suckers in the lake. It was also found in about 25 per cent of the suckers from the Cleveland mill pond. On the other hand, large suckers from the lake never have it. The largest suckers from the lake found to carry this parasite were only about 6 inches long. Infested suckers from the mill pond were somewhat larger, as much as 10 inches in length.

This is the first known instance of the occurrence of Octospinifer in New York State. Previously the genus has been known from Wisconsin, Michigan, and the Mississippi valley.

Family Rhadinorhynchidae

The most characteristic members of this family are parasites of marine fishes, their bodies provided with cuticular spines in addition to the hooks and spines developed on the proboscis. On the basis of general topography of the internal organs, one genus which occurs in both marine and fresh-water fishes is included within this family even though its representatives lack body spines. This is the genus Leptorhynchoides. Studies in progress at the present time, but not yet in form for presentation, support the assignment of this genus to the family Rhadinorhynchidae.

Genus Leptorhynchoides Kostylev, 1924

When Kostylev created the genus Leptorhynchoides with *L. plagicephalus*, a European species, as type, he listed as a possible additional species, *E. thecatus*, one of the most widely distributed and most generally known parasites of eastern North America. Subsequent studies by one of the present writers have verified this assignment.

PLATE 40

Plate 40. Acanthocephala of Oneida Lake Fishes. (The scales accompanying 3 and 5 have the value of 0.05 mm.) 1, *Neoechinorhynchus cylindratus*, anterior extremity of female. 2, *N. cylindratus*, posterior extremity of female. 3, Proboscis of *N. cylindratus*, showing arrangement of hooks. 4, *Octospinifer macilentus*, entire male. 5, Proboscis of *O. macilentus*, showing arrangement of hooks. 6, *Leptorhynchoides thecatus*, entire male. 7, *Pomphorhynchus bulbocolli*, entire male.

Leptorhynchoides thecatus (Linton, 1891)

Plate 40, Figure 6

Hosts.—*Micropterus dolomieu, Esox niger, E. lucius, Anguilla rostrata, Stizostedion vitreum, Ambloplites rupestris,* and occasionally in a long list of other species. In the intestine.

Specific Diagnosis.—Proboscis when fully extended not in line with axis of body but forming an angle with it. Males 7 mm. to 12 mm. long, females 11 mm. to 26 mm. Proboscis about 1 mm. long, armed with 12 longitudinal rows of 12 or 13 hooks each, each hook provided throughout much or all of its length with an ensheathing cuticular collar. Hooks near middle of proboscis about 0.071 mm. long; at anterior tip not so strong and less curved, about 0.077 mm. to 0.089 mm. long; those at base of proboscis nearly straight, 0.041 mm. to 0.053 mm. long. Lemnisci long and slender, about 1.5 times the length of proboscis receptacle. Embryos within body cavity of gravid female 0.080 mm. to 0.110 mm. long by 0.024 mm. to 0.030 mm. wide. Eight cement glands in male, closely compacted at posterior border of hind testis.

Micropterus dolomieu seems to be the most significant host of this species in Oneida Lake as well as in many other localities. In addition to the other normal hosts listed above, this species occurs in a long list of fishes, in some of which it never reaches full maturity. Encysted larval stages are very commonly encountered in the viscera of fishes.

A part of the life cycle has been determined for this species (Van Cleave, 1920:169). Larvae of *L. thecatus* have been found in both natural and experimental infestations of the amphipod, *Hyalella knickerbockeri*. Hyalella is very abundant in many parts of Oneida Lake and might well serve as host to *L. thecatus*, but experimental proof is lacking.

It seems probable that a larva too young to become established in the intestine of a fish that has swallowed the arthropod containing it, may actively penetrate the intestinal wall of the fish and proceed with larval growth in a cyst within the viscera. By such a means an additional intermediate host is linked into the chain of development. As such additional intermediate hosts of the larvae may be included those fishes which shelter the adult, as well as those which are never capable of bringing the worm to maturity.

The small-mouth black bass and the rock bass are very frequently heavily infested with *thecatus*,—about 75 per cent of the former and 50 per cent of the latter. In the two species of Esox, about 20 per cent of the individuals are infested, but with relatively small numbers of the worms.

Family Echinorhynchidae

No member of the genus Echinorhynchus, in the sense that this term is used at the present time, has been found in the Oneida Lake fauna. In fact, the only representative of this family found in the present survey is a species of the genus Pomphorhynchus.

Genus Pomphorhynchus Monticelli, 1905

The members of this genus are distinguishable from all other fish parasites by the presence of a long cylindrical neck between the body and the proboscis. At the distal end of this thin, cylindrical neck there is usually a large, spherical enlargement. This bulb is an accessory attachment organ, for though it lacks hooks or spines, the tissues of the host intestine grow around it and serve as an effective anchor to prevent dislodgment of the worm.

Only a single species has been recorded for North America and this is represented in the Oneida Lake fauna.

Pomphorhynchus bulbocolli Linkins, 1919

Plate 40, Figure 7

Hosts.—*Catostomus commersonnii, Cyprinus carpio, Erimyzon sucetta oblongus* and *Notemigonus crysoleucas;* in the intestine. Occasionally in other hosts.

Specific Diagnosis.—Body elongate, tapering toward the posterior end. Neck prominent, much smaller than anterior region of body to which it is attached, about 2.6 mm. to 4 mm. long, bearing a spherical enlargement about 0.8 mm. to 1.5 mm. in diameter at the anterior extremity of a practically cylindrical portion which is 0.15 mm. to 0.4 mm. in diameter. Proboscis 0.5 mm. to 0.6 mm. long by 0.07 mm. to 0.2 mm. in diameter, armed with 12 longitudinal rows of 12 to 14 hooks each; or expressed otherwise, with 24 to 28 circles of hooks of which the basal circle is composed of 12 hooks and the remaining ones of 6 each. Embryos within body cavity of gravid female 0.053 mm. to 0.083 mm. long and 0.008 mm. to 0.013 mm. in diameter.

The suckers and sucker-like fishes are the most frequent hosts of this species. About 60 per cent of *Erimyzon sucetta oblongus* were infested with it, and about 50 per cent of the carp and of the common sucker. Incidence in the golden shiner was somewhat lighter (about 30 per cent). The parasite also occurs occasionally in a number of other hosts where its presence is obviously accidental.

SECTION 6. ECOLOGY OF ONEIDA LAKE FISH PARASITES

The ecology of individual species of parasites has already been discussed in the preceding sections. In this section we shall concern ourselves with general considerations and a tabular presentation of some of the data collected in this survey.

Relative intensity of parasitism in various Oneida Lake fishes.—Our data on this subject are not conclusive because the numbers of the different fishes examined were very unequal. It is natural that where a great number of hosts are examined the list of parasite species encountered will be greater than where examinations are limited to only a few individuals. Allowance should be made for this fact in interpreting the tables, as well as for the fact that this survey applies only to Oneida Lake and only to the summer months.

One of the most important considerations for the ichthyologist with regard to parasitism is the question of what parasites occur in a particular host species, and whether these parasites are abundant or rare.

The following lists give our information on these points. We have indicated the frequency of occurrence, in the order: Abundant, Common, Occasional, Rare, and have attempted to make proper corrections for all factors which might create a false picture of the actual conditions.

We have placed little emphasis upon reporting new host records, since there are relatively few species of parasitic worms infesting fishes which may not occasionally find lodgment in any species of carnivorous fish of a given habitat.

In the Oneida Lake survey, the lamprey, which feeds upon the blood of fishes, has been found to harbor but a single species of worm parasite, a holostome larva in the eyes, which doubtless gains entrance by penetrating the body of its host. In contrast stand such forms as the yellow perch and the rock bass, for each of which more than twenty species of worms are recorded. Some of these parasites are known actively to penetrate the skin of the host, but the majority gain entrance with the food. Between the two extremes of susceptibility here mentioned, stand the majority of the fishes included in this survey.

As a general rule phylogenetically related fishes may be expected to carry similar parasitic populations. However, other factors, such as food habits, and habitat preferences frequently prove more important than the taxonomic relationships of the host in determining what kind of parasites occur.

Throughout the entire lists which follow in this section, an asterisk (*) preceding the name of a parasite indicates that the species does not attain maturity in the host cited. No differentiation is made between larvae carried normally by the fish as an essential part of the life cycle of the worm, and normal parasites of other fishes misplaced in an improper fish host. The reader is referred to the discussion of the individual species of parasites in an earlier section of this report, for details of these relationships.

Worm Parasites of Oneida Lake Fishes, Under Heading of Their Hosts

(* Indicates that parasite does not attain maturity in host cited.)

Lota maculosa

Common: Abothrium crassum, Spinitectus gracilis.

Occasional: *Diplostomulum scheuringi, *Diplostomulum sp., Azygia angusticauda, Neoechinorhynchus cylindratus, Leptorhynchoides thecatus, Pomphorhynchus bulbocolli.

Amia calva

Abundant: Haplobothrium globuliforme.

Common: Azygia longa, Proteocephalus perplexus.

Occasional: Neoechinorhynchus cylindratus.

Lepibema chrysops

Abundant: Allacanthochasmus varius.

Common: Allacanthochasmus artus.

Occasional: *Bucephalus (elegans type), *Diplostomulum sp., Proteocephalus pearsei, Neoechinorhynchus cylindratus, Leptorhynchoides thecatus.

Eupomotis gibbosus

Abundant: Spinitectus carolini.

Common: *Crepidostomum cornutum (abnormal), *Clinostomum marginatum, *Neascus vancleavei, *Proteocephalus ambloplitis, Capillaria catenata.

Occasional: *Diplostomulum scheuringi, Azygia angusticauda, Spinitectus gracilis, Neoechinorhynchus cylindratus, Leptorhynchoides thecatus, Pomphorhynchus bulbocolli.

Rare: *Haplobothrium globuliforme (cyst in liver), Spinitectus gracilis.

Pomoxis sparoides

Occasional: *Diplostomulum scheuringi, Spinitectus gracilis, Pomphorhynchus bulbocolli.

Ambloplites rupestris

Abundant: Crepidostomum cornutum.

Common: Bucephalus elegans, Cryptogonimus chyli, *Proteocephalus ambloplitis, Contracaecum brachyurum, Spinitectus carolini, Neoechinorhynchus cylindratus, Leptorhynchoides thecatus.

Occasional: Microphallus opacus, Microphallus ovatus, *Clinostomum marginatum, *Diplostomulum scheuringi, *Diplostomulum sp., *Neascus vancleavei, Azygia angusticauda, Capillaria catenata, Spinitectus gracilis, *Dichelyne cotylophora, Pomphorhynchus bulbocolli.

Rare: Alloglossidium corti,* Maritrema obstipum,* Maritrema medium, Camallanus oxycephalus.

Micropterus salmoides

Abundant: Neoechinorhynchus cylindratus.

Common: Rhipidocotyle papillosum, Caecincola parvulus, Azygia angusticauda, Contracaecum brachyurum, Leptorhynchoides thecatus.

Occasional: Crepidostomum cornutum, *Clinostomum marginatum, *Diplostomulum scheuringi, Capillaria catenata, Dichelyne cotylophora, Pomphorhynchus bulbocolli.

Rare: Phyllodistomum pearsei, Crepidostomum ictaluri, Bunodera sacculata, Neochasmus umbellus, *Hymenolepis sp.?

Micropterus dolomieu

Abundant: Neoechinorhynchus cylindratus, Leptorhynchoides thecatus.

Common: Rhipidocotyle papillosum, Crepidostomum cornutum, *Proteocephalus ambloplitis (larva).

Occasional: Cryptogonimus chyli, Centrovarium lobotes, Spinitectus carolini, Dichelyne cotylophora.

Rare: Phyllodistomum pearsei (doubtful), Azygia angusticauda, *Ligula intestinalis, Bothriocephalus claviceps, Proteocephalus ambloplitis (adult).

Umbra limi

Occasional?: *Neascus grandis, *Proteocephalus sp., *Nematode larva, type 3.

Rare ?: Gyrodactylus cylindriformis.

Leucosomus corporalis

Occasional: *Diplostomulum sp.

Pimephales promelas

Occasional?: *Clinostomum marginatum.

Fundulus diaphanus

Common: *Neascus vancleavei.

Hybognathus regius

Common: *Neascus vancleavei.

Occasional: *Ligula intestinalis.

Boleosoma nigrum olmstedi

Occasional: *Neascus vancleavei, Azygia angusticauda, *Ligula intestinalis, *Proteocephalus ambloplitis (larva), Neoechinorhynchus cylindratus, Leptorhynchoides thecatus.

Rare: Neochasmus umbellus.

Erimyzon sucetta oblongus

Common: Neoechinorhynchus cylindratus, Pomphorhynchus bulbocolli.

Rare: Hedruris tiara.

Catostomus commersonnii

Abundant: Pomphorhynchus bulbocolli.

Common: *Diplostomum flexicaudum, *Tetracotyle communis.

Occasional: Triganodistomum attenuatum, Triganodistomum simeri, *Clinostomum marginatum, Monobothrium ingens, Glaridacris catostomi, Glaridacris confusus, Biacetabulum infrequens, Octospinifer macilentus.

Rare: *Ligula intestinalis, Hepaticola bakeri, Philometra nodulosa.

Cyprinus carpio

Common: Dactylogyrus extensus, Pomphorhynchus bulbocolli.

Rare: Crepidostomum cooperi, Plagiocirrus primus, cestodarian (undetermined species).

Notemigonus crysoleucas

Common: Pomphorhynchus bulbocolli.

Occasional: Plagiocirrus primus, *Tetracotyle intermedia.

Rare: Crepidostomum cooperi, Hepaticola bakeri, *Nematode larva, type 3.

Percina caprodes zebra

Occasional: Crepidostomum isostomum, *Diplostomulum scheuringi, *Diplostomulum sp., *Tetracotyle sp., *Neascus vancleavei, Bothriocephalus formosus, Neoechinorhynchus cylindratus.

Rare: Phyllodistomum superbum (ectopic?), Azygia longa.

Perca flavescens

Abundant: *Diplostomum huronense (?), Dichelyne cotylophora.

Common: *Bucephalus (elegans type), Phyllodistomum superbum, Crepidostomum cooperi, *Clinostomum marginatum, *Diplostomulum scheuringi, *Neascus ambloplitis, Azygia angusticauda, *Spinitectus sp., Neoechinorhynchus cylindratus.

Occasional: Bunodera sacculata, Centrovarium lobotes, *Ligula intestinalis, Proteocephalus pearsei, *Proteocephalus ambloplitis, Philometra cylindracea, Leptorhynchoides thecatus.

Rare: Bunodera luciopercae, *Apophallus americanus, *Maritrema medium, *Camallanus oxycephalus, *Nematode larva type 3, Pomphorhynchus bulbocolli.

Stizostedion vitreum

Abundant: Bucephalopsis pusilla, Phyllodistomum superbum, Bothriocephalus cuspidatus, Neoechinorhynchus cylindratus.

Common: Ancyrocephalus aculeatus, *Spinitectus sp.

Occasional: Centrovarium lobotes, Sanguinicola occidentalis, Azygia angusticauda, *Triaenophorus nodulosus, Dichelyne cotylophora, Leptorhynchoides thecatus.

Rare: *Apophallus americanus, Proteocephalus macrocephalus, Capillaria catenata.

Salmo fario

Occasional: Phyllodistomum superbum, *Diplostomulum scheuringi, Azygia longa, Cystidicoloides harwoodi, Spinitectus gracilis, Neoechinorhynchus cylindratus.

Leucichthys artedi tullibee

Common: *Tetracotyle intermedia, Hepaticola bakeri.

Occasional: Crepidostomum cooperi, Spinitectus gracilis.

Percopsis omisco-maycus

Abundant: *Centrovarium lobotes (in cysts), *Diplostomum huronense.

Common: *Tetracotyle communis.

Occasional: Crepidostomum isostomum, Bothriocephalus formosus, *Triaenophorus robustus.

Rare: Phyllodistomum superbum (ectopic?).

Esox niger

Abundant: Spinitectus gracilis, Neoechinorhynchus cylindratus.

Common: *Bucephalus (elegans type), Macroderoides flavus, Proteocephalus pinguis, Leptorhynchoides thecatus.

Occasional: Microphallus ovatus, *Neascus amblopl itis, Azygia angusticauda, *Proteocephalus ambloplitis.

Rare: Hedruris tiara.

Esox lucius

Abundant: Proteocephalus pinguis.

Common: *Neascus ambloplitis, Neoechinorhynchus cylindratus.

Occasional: Tetraonchus monenteron, Leptorhynchoides thecatus.

Rare: Phyllodistomum superbum (ectopic?), Plagiocirrus primus, Spinitectus gracilis, Pomphorhynchus bulbocolli.

Ictalurus punctatus

Abundant: Vietosoma parvum.

Common: Crepidostomum ictaluri, Alloglossidium corti, Proteocephalus ambloplitis.

Occasional: Corallobothrium fimbriatum.

Schilbeodes gyrinus

Abundant: Alloglossidium corti.

Occasional: Corallobothrium fimbriatum.

Schilbeodes miurus

Occasional: Alloglossidium corti, *Diplostomulum sp.

Ameiurus nebulosus

Abundant: Alloglossidium geminus, Corallobothrium fimbriatum.

Common: Acetodextra amiuri, *Proteocephalus ambloplitis, Dichelyne robusta.

Occasional: Ancyrocephalus sp., *Bucephalus (elegans type), Phyllodistomum staffordi, Crepidostomum cornutum, Crepidostomum cooperi, Crepidostomum ictaluri, Alloglossidium corti, Spinitectus gracilis, Leptorhynchoides thecatus, Pomphorhynchus bulbocolli.

Rare: Allocreadium halli, Cryptogonimus chyli, Microphallus opacus, *Dichelyne cotylophora.

Ameiurus natalis

Occasional: Crepidostomum cornutum, Crepidostomum ictaluri, Alloglossidium corti, Alloglossidium geminus, Acetodextra amiuri, *Diplostomulum sp., Corallobothrium fimbriatum, Dichelyne robusta, Neoechinorhynchus cylindratus, Leptorhynchoides thecatus.

Rare: Centrovarium lobotes.

Noturus flavus

Abundant (?): Crepidostomum ictaluri.

Occasional (?): Leptorhynchoides thecatus.

Anguilla rostrata

Abundant: Azygia longa.

Common: Bothriocephalus claviceps, Proteocephalus macrocephalus, Haplonema sp., Leptorhynchoides thecatus.

Occasional: *Diplostomulum sp., Neoechinorhynchus cylindratus.

Host-Parasite Relationships of Oneida Lake Fish Parasites

In the long list of parasites we have gathered some are obviously very well established in the lake so that they occur in their particular hosts with a high incidence, and frequently in great numbers in a single infestation. Some of these worms are evidently able to infest, and grow to maturity in, a number of different hosts, but in this case a particular host species is usually found to be the most favorable one, as shown by greater frequency and intensity of infestation and also by the thriving appearance of worms from such a host. This particular host is in such cases to be regarded as the natural host of the parasite, which passes only incidentally to other hosts capable of supporting it. A list of the commoner parasites and their natural hosts follows on pages 322 and 323. On page 323 is given a list of parasites apparently adapted to a wide range of hosts, and on pages 323 and 324, a list of those parasites that are more or less clearly limited to a single host. Further facts on the relationships of all of these parasites have been given in the systematic section.

A List of the Commoner Parasites of Oneida Lake Fishes and Their Natural Hosts

(The parasites are listed in their systematic order.)

Trematoda

1. Dactylogyrus extensus	Cyprinus carpio
2. Ancyrocephalus aculeatus	Stizostedion vitreum
3. Bucephalopsis pusilla	Stizostedion vitreum
4. Bucephalus elegans	Ambloplites rupestris
5. Rhipidocotyle papillosum	Micropterus dolomieu and M. salmoides
6. Phyllodistomum superbum	P. flavescens and S. vitreum
7. Phyllodistomum staffordi	Ameiurus nebulosus
8. Crepidostomum cornutum	Ambloplites rupestris
9. Crepidostomum cooperi	Perca flavescens
10. Macroderoides flavus	Esox niger
11. Alloglossidium corti	Schilbeodes gyrinus
12. Alloglossidium geminus	Ameiurus nebulosus
13. Acetodextra amiuri	Ameiurus nebulosus
14. Victosoma parvum	Ictalurus punctatus
15. Cryptogonimus chyli	Ambloplites rupestris
16. Caecincola parvulus	Micropterus salmoides
17. Allacanthochasmus varius	Lepibema chrysops
18. *Clinostomum marginatum	Perca flavescens
19. Sanguinicola occidentalis	Stizostedion vitreum
20. *Diplostomum flexicaudum	Catostomus commersonnii
21. *Diplostomum huronense	Percopsis, Perca flavescens
22. *Tetracotyle communis	Catostomus commersonnii
23. *Neascus vancleavei	Eupomotis gibbosus
24. *Neascus amblopltis	Perca flavescens
25. Azygia longa	Anguilla rostrata
26. Azygia angusticauda	Perca flavescens

Cestoda

27. Haplobothrium globuliforme	Amia calva
28. Bothriocephalus cuspidatus	Stizostedion vitreum
29. Bothriocephalus claviceps	Anguilla rostrata
30. Abothrium crassum	Lota maculosa
31. Proteocephalus pinguis	Esox niger
32. *Proteocephalus ambloplitis	Numerous fishes
33. Corallobothrium fimbriatum	Ameiurus nebulosus

Nematoda

34. Capillaria catenata	Eupomotis gibbosus
35. Contracaecum brachyurum	Micropterus salmoides
36. Spinitectus carolini	Eupomotis gibbosus
37. Spinitectus gracilis	Esox niger
38. Dichelyne cotylophora	Perca flavescens
39. Haplonema sp.	Anguilla rostrata
40. Philometra cylindracea	Perca flavescens

Acanthocephala

41. Neoechinorhynchus cylindratus	Micropterus salmoides
42. Leptorhynchoides thecatus	Micropterus dolomieu
43. Pomphorhynchus bulbocolli	Catostomus commersonnii
44. Octospinifer macilentus	Catostomus commersonnii

A List of the Commoner Parasites of Oneida Lake Fishes that Show Adaptation to a Wide Variety of Hosts

1 Crepidostomum cornutum
2. *Clinostomum marginatum
3. *Diplostomulum scheuringi
4. *Diplostomulum (various species)
5. *Tetracotyle (various species)
6. *Neascus vancleavei
7. *Neascus ambloplitis
8. Azygia angusticauda
9. *Proteocephalus ambloplitis
10. Corallobothrium fimbriatum (in various silurids)
11. Spinitectus carolini
12. Spinitectus gracilis
13. Neoechinorhynchus cylindratus
14. Leptorhynchoides thecatus
15. Pomphorhynchus bulbocolli

A List of Parasites Limited More or Less Strictly to a Single Host for Completing their Sexual Development

Trematoda

Parasite	*Host*
1. Gyrodactylus cylindriformis	Umbra limi
2. Dactylogyrus extensus	Cyprinus carpio
3. Ancyrocephalus aculeatus	Stizostedion vitreum
4. Tetraonchus monenteron	Esox lucius
5. Bucephalopsis pusilla	Stizostedion vitreum
6. Bucephalus elegans	Ambloplites rupestris
7. Rhipidocotyle papillosum	Micropterus salmoides
8. Phyllodistomum staffordi	Ameiurus nebulosus
9. Allocreadium ictaluri	Ameiurus nebulosus
10. Triganodistomum attenuatum	Catostomus commersonnii
11. Triganodistomum simeri	Catostomus commersonnii
12. Macroderoides flavus	Esox niger
13. Vietosoma parvum	Ictalurus punctatus
14. Caecincola parvulus	Micropterus salmoides
15. Allacanthochasmus varius	Lepibema chrysops
16. Allacanthochasmus artus	Lepibema chrysops
17. Sanguinicola occidentalis	Stizostedion vitreum
18. *Neascus grandis	Umbra limi

Cestoda

19. Glaridacris catostomi	Catostomus commersonnii
20. Glaridacris confusus	Catostomus commersonnii
21. Bothriocephalus cuspidatus	Stizostedion vitreum
22. Bothriocephalus claviceps	Anguilla rostrata
23. Abothrium crassum	Lota maculosa
24. Haplobothrium globuliforme	Amia calva
25. Proteocephalus macrocephalus	Anguilla rostrata
26. Proteocephalus perplexus	Amia calva

Nematoda

27. Cystidicoloides harwoodi	Salmo fario
28. Dichelyne cotylophora	Perca flavescens
29. Haplonema sp.	Anguilla rostrata
30. Philometra cylindracea	Perca flavescens
31. Philometra nodulosa	Catostomus commersonnii

Acanthocephala

32. Octospinifer macilentus	Catostomus commersonnii

Parasites of Rare Occurrence in Oneida Lake Fishes.—A number of parasites which have been treated in this report have been encountered in so few instances as to indicate that they are actually rare in this lake. Possibly these parasites are more numerous in adjacent bodies of water, which we have not studied, and from which they are occasionally borne into the lake. In some cases it is certain these parasites (Apophallus, Maritrema) do not belong in fishes but have a mammal or bird as definitive host. In other cases *(Camallanus oxycephalus, Bunodera luciopercæ, Proteocephalus pearsei)* these parasites are known to occur with frequency in other bodies of water. In the case of *Neochasmus umbellus, Apophallus americanus, Hymenolepis sp., Hedruris tiara,* we are dealing with parasites in regard to which only the most meagre information of any kind is available.

A List of Parasites of Decidedly Rare Occurrence in Oneida Lake Fishes

Trematodes	No. specimens in our collections
1. Phyllodistomum pearsei	1
2. Bunodera luciopercae	1
3. Neochasmus umbellus	10
4. *Apophallus americanus	2
5. *Maritrema obstipum	1
Cestodes	
6. *Hymenolepis sp.?	1
Nematodes	
7. Hedruris tiara	2
8. Camallanus oxycephalus	4 (2 larval)
9. Philometra nodulosa	1

Correlation of Parasitism and Habitat.—Certain parasites are very clearly restricted in their occurrence to certain habitats in the lake. In many cases too little is known of the life history of the worms to explain just what factors may determine this differential distribution, but in most cases it may be surmised that it is co-extensive with the range of the intermediate host. In compiling Table No. 3 we have omitted cases in which a parasite is more or less clearly limited to a single definitive host, and this host in turn limited to a single type of habitat, for in such cases it is not possible to tell whether the parasite may be influenced in its distribution solely by the availability of its definitive host, or may be adjusted also to other environmental factors. Parasites not mentioned in this list are either of uncertain correlations or of general distribution, some of the latter being included in the table for purposes of contrast.

This aspect of our work has disclosed the interesting fact that in fishes of wide range through a variety of environmental types, the type of parasitism is more or less closely correlated with the habitat from which the fish is taken. This can only be interpreted to indicate that in general these fishes are not freely migratory in spite of their wide range, but that individuals confine their movements more or less definitely within a particular habitat. In some instances we are even convinced that the fishes within any particular small bay or shore-line locality must remain rather definitely within that locality—their "home range." This is indicated by the fact that the parasitic fauna of the same species of fish taken from two adjacent but dissimilar localities is frequently markedly different.

In the case of the perch two distinct groups occur, namely, those from the deep water (30-50 feet) and those from shallow water (shore-line localities). This separation of the two groups of perch is shown in the differences between their parasitic faunas, as shown in the list below.

Table No. 3. Oneida Lake Fish Parasites Showing a Definite Correlation with Habitat Types

	Habitat types: Oneida Lake							Tributary types	
	General Distribution	Shallow Water	Deep Water	Mud Bottom	Hard Bottom	Protected Shoreline	Open Water	Trout Streams	Slow Streams
Crepidostomum cornutum					*		*		
Crepidostomum cooperi	*								
Bunodera sacculata		*				*			
Alloglossidium corti			*						*
Alloglossidium geminus						*			
Cryptogonimus chyli					*		*		
Caecincola parvulus		*				*			
*Clinostomum marginatum		*				*			
*Diplostomulum (all sp.)	*								
*Tetracotyle (all sp.)			*				*		
*Neascus amblopitis		*				*			
Azygia longa			*				*		
Azygia angusticauda		*				*			
Cestodaria (all species)				*					
Bothriocephalus (all sp.)	*								
Proteocephalus (all sp.)	*								
Corallobothrium fimbriatum	*								
Contracaecum brachyurum		*				*			
Cystidicoloides harwoodi								*	
Spinitectus carolini		*							
Spinitectus gracilis				*					
Dichelyne cotylophora	*								
Philometra cylindracea			*				*		
Neoechinorhynchus cylindratus	*								
Leptorhynchoides thecatus	*								
Pomphorhynchus bulbocolli		*		*					

List of Parasites of the Perch Showing a Differential Incidence Correlated with Habitat of the Host within the Lake

From Protected Shore Waters chiefly and Seldom or Never from Deep Water.	From Open Deep Water chiefly and Seldom or Never from Shallow Water.
Bunodera sacculata	—
*Clinostomum marginatum	—
*Neascus amblopitis	—
Azygia angusticauda	—
—	Philometra cylindracea

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PART IV. ADDITIONAL NOTES ON PARASITES OF ONEIDA LAKE FISHES, INCLUDING DESCRIPTIONS OF NEW SPECIES

By Justus F. Mueller

CONTENTS

SECTION 1. A RESTUDY OF THE HETEROPHYIDAE AND CERTAIN OTHER TREMATODES FROM NORTH AMERICAN FISHES

Mueller and Van Cleave (1932) brought together under the family Heterophyidae a number of fish trematodes which had previously been assigned to diverse places in the classification. This paper was based on the gross features of the forms included, and at that time there was no evidence as to what extent the detailed anatomy of these forms supported the conclusions drawn. Of the genera considered, only the genus Cryptogonimus had previously been studied with any attempt at completeness of detail. Osborn (1910) had made a study of this form from sections, but, as will be shown later, his account was incorrect in certain important points. The genus Vietosoma was assigned to the Heterophyidae by Mueller and Van Cleave mainly on the basis of its apparent similarity to Euryhelmis, which studies of Baer (1931) had definitely shown to be heterophyid. A restudy of Vietosoma has proved this action in error, for a definite cirrus sac occurs in this genus at the usual position, and hence the worm is excluded from the Heterophyidae. All of the genera included in our original paper have received restudy in the present paper except Neochasmus. Because of its rarity, additional material of this form could not be obtained.

In addition to the Heterophyidae a number of genera of fish trematodes have been described which lack a cirrus sac. Among these may be mentioned Microphallus, Azygia, Halipegus, Anallocreadium, and Microcreadium. Microphallus, Halipegus, and Azygia are sufficiently well understood to be excluded with certainty from the Heterophyidae. But some of the others appeared open to question. The genus Anallocreadium, Simer, 1929, was not encountered in Oneida Lake, but material of the species *Anallocreadium pearsei*, from *Aplodinotus grunniens*, was kindly lent the writer by Dr. George W. Hunter. This was studied to determine possible affinities with the Heterophyidae.

Anallocreadium pearsei Hunter and Bangham, 1932

I am able to confirm the previous conclusions of Simer (1929) and Hunter and Bangham (1932). The worm is not related to the Heterophyidae, and doubtless belongs to the Allocreadiidae, where these authors have placed it. My observations verify the fact that the excretory bladder is sac-like, without bifurcation, entirely restricted to the post-testicular region. The description of the female reproductive system, given by Hunter and Bangham, has been checked, and supplemented with a composite diagram of this system as seen in transverse sections, Plate 46, Figure 10. The prostate cells are few in number, and closely compressed against the male duct, unlike the condition found in the Heterophyidae.

Genus Microcreadium Simer, 1929

This genus rests on a single species, *M. parvum* Simer, 1929. No material of this species was available for study, but from Simer's rather complete description it appears that Microcreadium is related to Anallocreadium, and no doubt belongs with this genus in the subfamily Anallocreadiinae, Hunter and Bangham, 1932.

Vietosoma parvum Van Cleave and Mueller, 1932

Plate 44, Figures 8–10

This species was first assigned by the authors to the Plagiorchiidae, Reniferinae. From observations on toto mounts a cirrus sac was said to be present. Mueller and Van Cleave (1932) transferred the form to the Heterophyidae, Heterophyinae, on the basis of its marked resemblance in general features to Euryhelmis. At this time it was stated that "structures which were interpreted as cirrus and cirrus sac were described for Vietosoma, but in rechecking our material we have discovered that these structures were misinterpreted, and that in plan of organization the ventro-genital sac of Vietosoma is distinctly heterophyid." The sections available at the time of this study had been prepared by a student assistant, and were very poor and apparently incomplete. Upon restudy of this species from better material it is evident that the original observations of Van Cleave and Mueller were correct. A cirrus sac is present. The seminal vesicle is divided into two chambers. The pars prostatica is small, the prostate cells closely packed, and the terminal portion appears faintly muscular. The uterus opens into the common genital pore adjacent to the tip of the cirrus, and passes backward on one side of the acetabulum toward the posterior end of the body along the ventral surface.

The ovary is dorsal. The oviduct loops sharply to the right and gives off an anterior and posterior branch. The posterior branch curves posteriad and mesiad, and opens to the surface as Laurer's canal. The anterior branch is immediately joined by the common yolk duct, and passes ventrad as the ootype and neck of the uterus. The yolk reservoir lies posterior to the neck of the uterus, its transverse ducts passing ventral to the crura. The neck of the uterus continues posteriad along the ventral surface parallel to the ascending terminal limb of the uterus. The shell gland surrounds the ootype just beyond the entrance of the yolk duct. A seminal receptacle is lacking.

In the original description Van Cleave and Mueller stated that the excretory bladder is Y-shaped in younger specimens, but acquires a number of accessory branches in older worms. This statement, made on the basis of a study of whole mounts, appears erroneous in the light of further study. Serial sections show that the excretory bladder extends forward as an unbranched tubular trunk between the testes to the level of the ootype, and here there is only a very slight trace of bifurcation, which, however, may be interpreted as the vestige of an originally Y-shaped condition. However, no accessory branches can be discovered on restudy, and it appears that what we represented as such in our figures 5 and 6, Plate I, were empty branches of the uterus which in optical section were misinterpreted as arising from the excretory bladder.

These unfortunate misinterpretations and consequent shiftings of Vietosoma are more easily understood when the minute size of the worm is taken into consideration. Moreover, its striking similarity in general features to Euryhelmis was naturally misleading. In the preceding paper by Van Cleave and Mueller, on the basis of evidence set forth in the present study, the genus was restored to its original position under the Plagiorchiidae, Reniferinae, and here it doubtless belongs. The character of the female reproductive system, and the presence of a cirrus sac, are sufficient to exclude it definitely from the Heterophyidae.

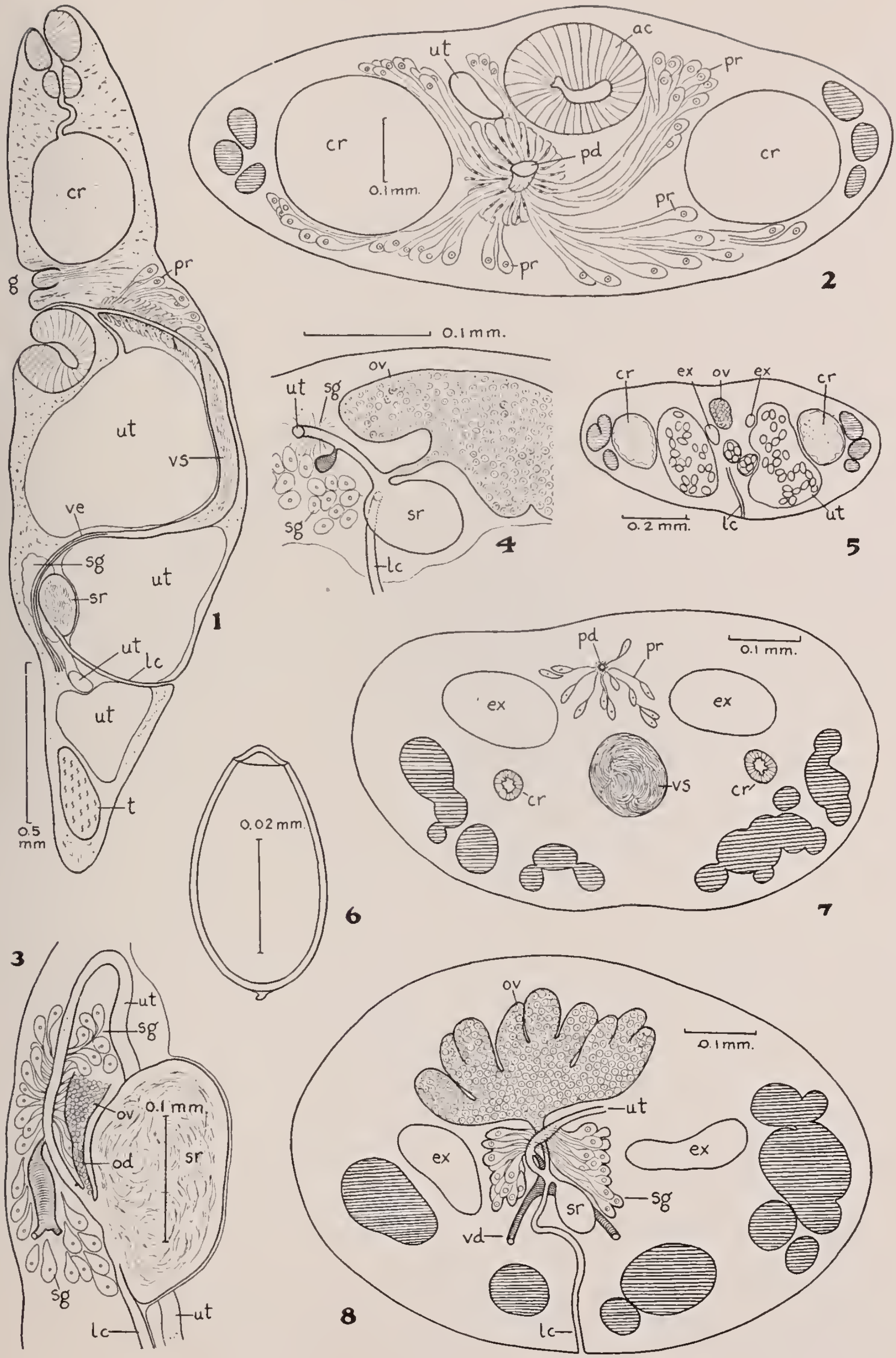
Plate 41. Heterophyinae.

Acetodextra amiuri. 1, Composite sagittal section showing path of seminal vesicle, Laurer's canal, and prostate part of male duct. 2, Cross section through acetabulum showing location of prostate cells. 3, Sagittal section composite of female genitalia. 4, Cross section composite of female genitalia. 5, Cross section through opening of Laurer's canal. 6, Egg.

Centrovarium lobotes. 7, Cross section through prostate region. 8, Composite cross section of female genitalia.

ac—acetabulum, cr—crura, ex—excretory bladder, g—gonotyl, lc—Laurer's canal, od—oviduct, ov—ovary, pd—prostate portion of male duct, pr—prostate cells, sg—shell gland, sr—seminal receptacle, t—testis, ut—uterus, vd—vas deferens, ve—vas efferens, vs—seminal vesicle.

PLATE 41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Family Heterophyidae. Subfamily Heterophyinae Ciurea, 1924

Acetodextra amiuri (Stafford, 1900)

Plate 41, Figures 1–6

The excretory pore is terminal. The Y-shaped excretory bladder passes forward as a single trunk between the testes. At the anterior border of the testes this trunk branches into two lateral horns, of small diameter, which pass anteriad interior to the crura. At the level of the ovary these become too small to be followed further in sections.

The ovary and its associated structures are pressed against the ventral surface beneath the folds of the uterus. The seminal receptacle lies on the dorsal aspect of the ovary. Ovary flattened, with seven or eight small marginal lobes. The cells of the shell gland are clustered in a large area on the dorsal aspect of the ovary, above its left margin and to the left of the seminal receptacle. The oviduct arises from the dorsal side of the ovary, near its center, and passes left to join the seminal receptacle. The typiduct reverses direction in a V and continues a short distance to the left, and anteriad. Opposite the edge of the ovary it is joined by the yolk duct, and then passes into the ootype, which is surrounded by the shell gland for a distance of 0.100 mm. The uterus continues forward, then loops and passes backward, and after some preliminary winding enlarges into the characteristic form of the organ along most of its course. Laurer's canal arises from the ventral surface of the seminal receptacle, posterior to the entrance of the oviduct. It passes backward at an angle, gradually curves dorsally, passing between the folds of the uterus, and emerges on the dorsal surface, at about the level of the posterior edge of the ovary, in the median line. The transverse yolk ducts pass mediad dorsal to the crura, swing around the uterine mass internal to the crura, and pass ventrad to the yolk reservoir. The vitellaria are completely restricted to the lateral fields, external to the crura. The uterus and crura are very voluminous, constituting most of the bulk of the worm.

The vasa efferentia ascend ventrally on the left of the ootype, and anterior to the ovary pass obliquely toward the dorsal surface to join the seminal vesicle, which is bent ventrad to meet them. The male duct is divided into a dilated seminal vesicle and a prostatic portion. The prostatic portion is surrounded by a layer of cells divisible into an anterior and a posterior region. In the anterior region the surrounding cells are of two kinds, (1) a series of small cells with spindle shaped nuclei, which lie in the interstices of the necks of the large cells, and (2) a series of large prostatic cells the bodies of which lie peripherally near the surface of the body, their long necks reaching in to empty into the prostate portion of the male duct. These cells have vesicular nuclei with a large nucleolus. In the posterior part of the prostate region only the second type of cells occurs. The metraterm joins the ejaculatory duct anterior to its prostate portion, and the common genital duct proceeds to the pore between the gonotyl and acetabulum as previously described. The metraterm enters the common genital duct from the left side.

The parenchyma is weak, and the suckers only feebly muscular. The cuticula is smooth and devoid of spines. The eggs are straw colored, jug shaped, with very distinct opercula, about 0.040 mm. long, by 0.020 mm. wide.

Cryptogonimus chyli Osborn, 1903

Plate 42, Figures 8–14

This worm is completely covered with small rounded spines, very closely set, and much smaller than represented by Osborn. The ovary is ventral, and has seven or eight lobes, sometimes less. The seminal receptacle lies near the dorsal surface. The oviduct proceeds dorsally toward the seminal receptacle, and short of this organ gives off a recurrent branch, the typiduct. This is shortly joined by the yolk duct and passes into the ootype. The cells of the shell gland lie in a loose cluster chiefly anterior to the ootype. They are not peripheral as in *Allacanthochasmus artus*. Laurer's canal is very long, and extends almost straight back to open on the mid dorsal surface near the posterior tip of the second testis.

The transverse yolk ducts slant backward toward the yolk reservoir as in Cæcincola. The neck of the uterus passes over the anterior surface of the oviduct from the left, and posteriad. The egg is dark brown, elliptical, about 0.022 mm. x 0.012 mm., and has a polygonal sculpturing as in Cæcincola.

The gonotyl and acetabulum lie within a deep sinus, the lip of which possesses a distinct sphincter. The genital cloaca opens between gonotyl and acetabulum, but is surrounded by the posterior edge of the gonotyl. The gonotyl and acetabulum differ in structure. The acetabulum possesses numerous nuclei and a regular cup like form, whereas the gonotyl has very few nuclei, and has tapering internal edges or roots. A broad compressed cavity lies between acetabulum and gonotyl, and the common genital duct opens at its bottom. The cloaca branches dorsal to the gonotyl, the uterus forming the left branch, the male system the right. The male system has a small prostate chamber, separated by a constriction from the seminal vesicle. The prostate chamber has papillose walls, formed by the tips of the prostatic cells. These cells lie peripherally near the dorsal surface, and are much longer than Osborn shows in his figure. They have empty-looking cytoplasm, and centrally located nuclei.

The excretory bladder is Y-shaped, dilated throughout. The fork occurs posterior to the ootype. The posterior stem lies centrally between the coils of the uterus, dorso-ventrally compressed. The anterior branches reach forward to the pharyngeal level.

The description by Osborn (1910) is incorrect in regard to the seminal receptacle, Laurer's canal, the character of the gonotyl, and certain other details such as the character of the cuticular spines.

Caecincola parvulus Marshall and Gilbert, 1905

Plate 42, Figures 1–7

Mueller and Van Cleave (1932), following previous authors, affirmed the similarity between Cryptogonimus and Caecincola. This conclusion is supported by further study.

The ovary lies ventrally, and is usually divided into three lobes, but occasionally the beginning of a fourth lobe is visible. The oviduct passes toward the dorsal surface, and slightly anteriad, where it meets the seminal receptacle. The seminal receptacle lies dorsally, slightly anterior to the ovary, and is likely to be mistaken for a terminal compartment of the seminal vesicle. At its connection with the

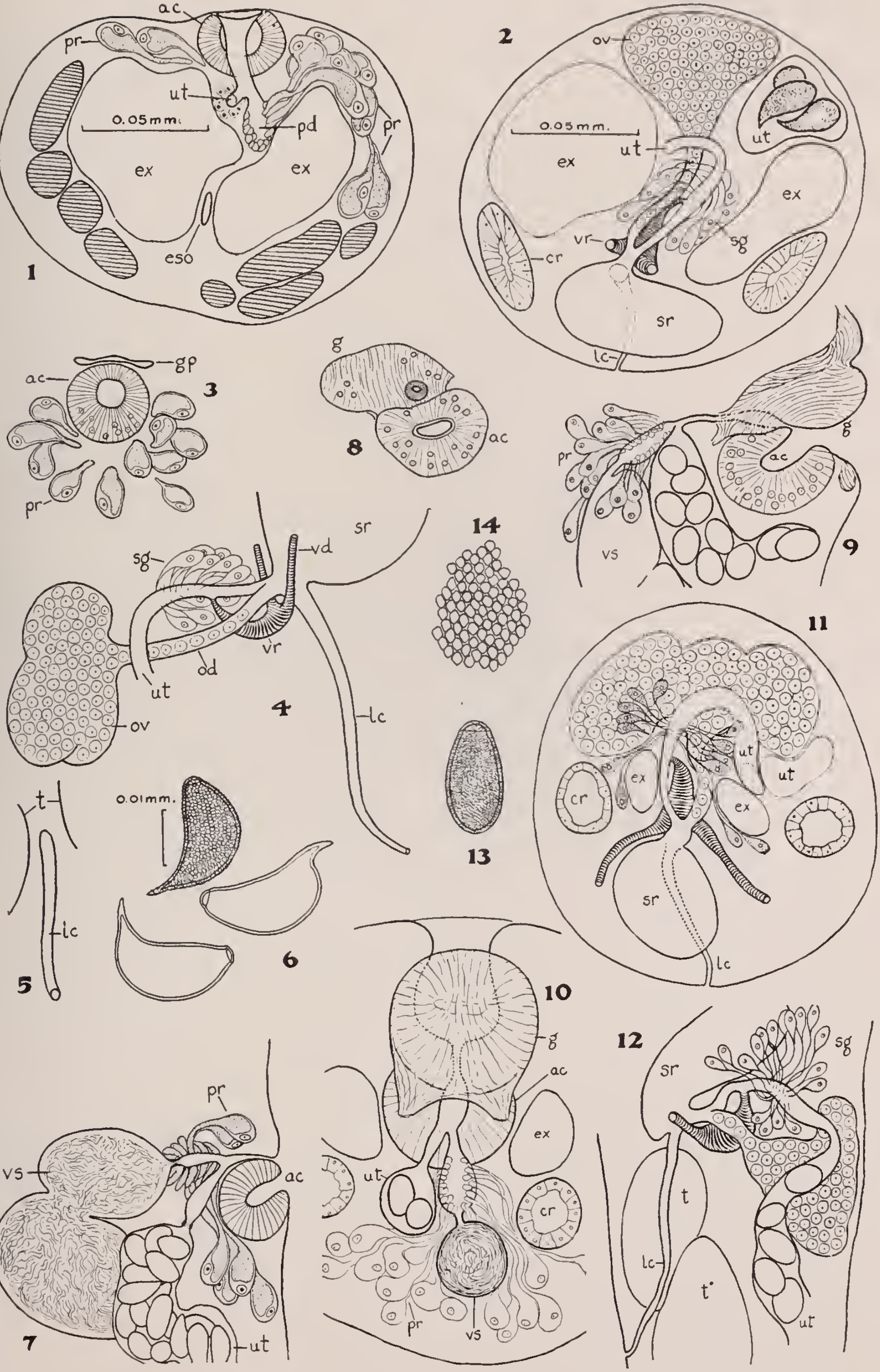
Plate 42. Heterophyinae (scales with Figs. 1 and 2 apply to all figures except 6, 13, and 14. Figs. 13 and 14 on same scale as Fig. 6.)

Caecincola parvulus. 1, Cross section through common genital duct, on anterior edge of acetabulum. 2, Cross section composite of female genitalia. 3, Detail of frontal section of acetabulum, near surface, showing width of genital cloaca, and prostate cells. 4, Diagram of female genitalia, from left. 5, Frontal section detail of Laurer's canal, approaching surface, between testes. 6, Eggs, upper showing surface sculpturing. 7, Sagittal composite through genital pore.

Cryptogonimus chyli. 8, Frontal section acetabulum and gonotyl showing common genital duct perforating the gonotyl. 9, Sagittal section composite region of genital pore. 10, Transverse section composite showing gonotyl, acetabulum, common genital duct, etc. 11, Transverse section composite of female genitalia. 12, Sagittal section composite female genitalia. 13, Egg. 14, Spines from head region.

ac—acetabulum, cr—crura, eso—esophagus, ex—excretory bladder, gp—genital pore, lc—Laurer's canal, od—oviduct, ov—ovary, os—oral sucker, pd—prostate portion of male duct, ph—pharynx, pr—prostate cells, sg—shell gland, sr—seminal receptacle, t—testes, ut—uterus, vd—yolk duct, vr—yolk reservoir, vs—seminal vesicle.

PLATE 42



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seminal receptacle the oviduct recurves sharply toward the ventral surface to form the typiduct. This is joined by the yolk duct and passes into the ootype and the uterus. The yolk reservoir lies posterior to these organs, its two lateral ducts passing forward on either side of the seminal receptacle. From the posterior aspect of the seminal receptacle arises Laurer's canal, which passes very far posteriad in the dorsal angle between the two testes, before it opens to the dorsal surface, near the mid line as in Cryptogonimus. The shell gland consists of a cluster of large pyriform cells, centrally located.

The prostate cells are pyriform, and hollow, containing a large internal reservoir. Their long necks reach to the prostatic portion of the male duct, and impart a papillose character to its inner wall. The prostate chamber is separated from the seminal vesicle by a slight constriction, as in Cryptogonimus. The prostate cells lie chiefly on the ventral surface on either side of the acetabulum, in contrast to Cryptogonimus, where they lie dorsally. The common genital duct is wide, and passes over the anterior surface of the acetabulum before it branches. The metraterm passes slightly to the left, the male duct to the right. A gonotyl is completely lacking.

The excretory system is Y-shaped; all three of its arms dilated. The division occurs posterior to the ovary, and the anterior arms reach to the head region. The posterior stem of the excretory bladder lies between the dorsally placed testes and the ventral coils of the uterus.

The egg is 0.023 mm. long by 0.011 mm. wide, with the anopercular end drawn out sidewise into a long point, in contrast to the ovoidal egg of Cryptogonimus. But the shell is dark brown in color, and has polygonal surface sculpturing as in Cryptogonimus. The surface of the worm is covered with spines, but these are so small that they appear as mere dots under the oil immersion lens.

Points of similarity between Cryptogonimus and Cæcincola are: general size and topography of organs, character of the female reproductive system, the path of Laurer's canal, and the dark color and sculptured shell of the eggs. The two are dissimilar in the absence of the gonotyl in Cæcincola; the much coarser spines of Cryptogonimus, and the shape of the egg, which has a tail in Cæcincola, but is rounded in Cryptogonimus. In both forms the shell gland is centrally located, and the prostatic cells are peripheral. While the two are alike in many respects, the differences are as marked as the similarities, and what relationship exists is not as close as would at first appear.

Centrovarium lobotes (MacCallum, 1895)

Plate 41, Figures 7–8

Mueller and Van Cleave (1932) postulated a relationship between Centrovarium and Cæcincola on the basis of agreement in general morphology. The present study of Centrovarium was made on adolescaria from cysts in the muscles of the trout perch. These adolescaria are fully as large as the sexually mature worms, show the organ system more clearly, and occasionally have a few precocious eggs in the uterus.

The ovary is ventral. The oviduct arises centrally from the dorsal side of the ovary, and passes anteriad and dorsad to join the seminal receptacle at a right angle. Opposite the oviduct Laurer's canal passes to the mid line of the dorsal surface, its external opening slightly posteriad of its internal end. The seminal receptacle lies anterior to this complex. Opposite its opening, the typiduct emerges, passes to the left and is joined by the yolk duct. The ootype makes an arcuate sweep, and merges into the neck of the uterus, which curves over the anterior surface of the oviduct, and begins its descent on the right. The yolk reservoir is posterior to the complex, its lateral ducts converging backward to meet it in a V, one branch on either side of the seminal receptacle. The cells of the shell gland form a centrally located compact cluster. The ovary is highly lobate, its rosetted lobes united by a central mass. The vitellaria are chiefly lateral, converging toward the mid-dorsal line.

The excretory bladder is Y-shaped, with the pore terminal. All three of its arms are widely dilated. The fork occurs back of the ovary, and the two anterior arms terminate at the level of the pharynx.

The terminal apparatus of the male system lies partly anterior to the acetabulum. The seminal vesicle is large, and its anterior extremity gives rise to a narrow duct which passes ventrad and posteriad to form the prostatic portion. The prostate cells surround the entire terminal portion of the male duct, but in this form they are small, and their bodies lie in the vicinity of the duct, never widely removed in the peripheral regions. They are few and scattered, with eccentric pyriform nuclei. The common genital duct passes inward over the anterior face of the acetabulum, and at once branches into the male duct which passes anteriad, and the metraterm, which passes posteriad.

In the adolescaria the seminal vesicle is already filled with sperms, but the seminal receptacle is empty.

The egg of *Centrovarium lobotes* is similar to that of Acetodextra, but completely lacks a terminal papilla. It is 0.017 mm. by 0.008 mm. in diameter.

Family Heterophyidae. Subfamily Neochasminae

Van Cleave and Mueller, 1932

Allacanthochasmus artus Mueller and Van Cleave, 1932

Plate 43, Figures 6–12

The body is almost circular in cross section, and the cuticula is covered with spines, much more delicate than those of *A. varius,* which completely surround the body. The lobate ovary occupies a broad semicircle around the ventral surface of the body. The oviduct arises from the dorsal surface of the ovary near the center of the cross section of the body, and passes anteriad a short distance to join the seminal receptacle opposite the origin of Laurer's canal. Laurer's canal passes backward and opens to the surface just posteriad to the level of the origin of the oviduct. The transverse vitelline ducts pass obliquely backward to the corners of the yolk reservoir, which lies posterior to the seminal receptacle, in the angle between the oviduct and Laurer's canal. The common yolk duct arises on the ventral corner of the yolk reservoir and passes to the typiduct. The seminal receptacle is large, equal in diameter to about one-half that of the body, and lies dorsally, anterior to the ovary.

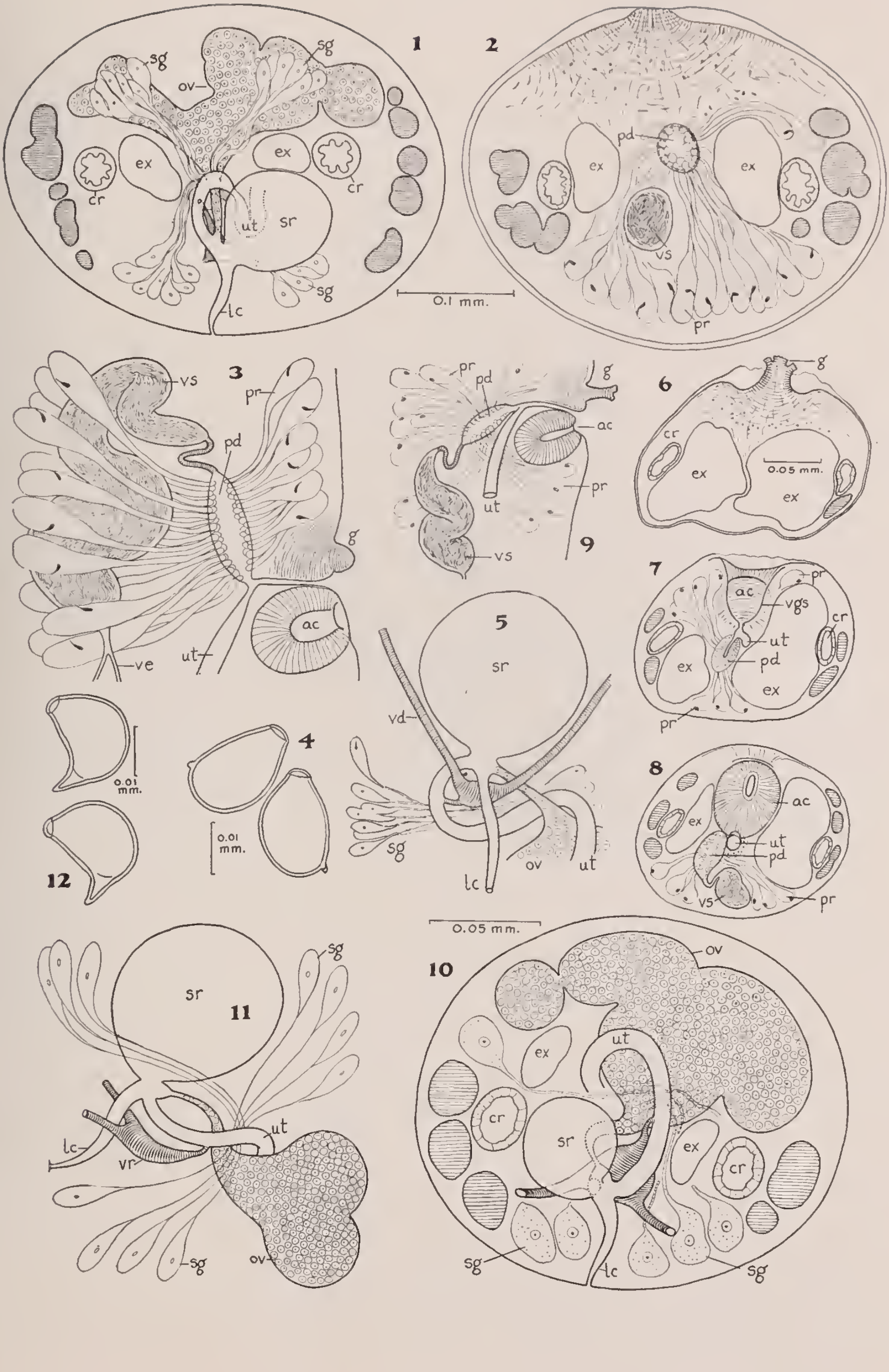
Plate 43. Neochasminae.

Allacanthochasmus varius. 1, Composite cross section of female genitalia. 2, Cross section through prostate cells. 3, Diagram of male duct and relation to genital pore. 4, Eggs. 5, Diagram of female genitalia seen from dorsal side.

Allacanthochasmus artus. 6, 7, 8, Successive cross sections through gonotyl, genital pore, and acetabulum. 9, Diagram of male duct. 10, Composite cross section of female genitalia. 11, Diagram of female genitalia seen from right. 12, Eggs.

ac—acetabulum, cr—crura, ex—excretory bladder, g—gonotyl, lc—Laurer's canal, ov—ovary, pd—prostate portion of male duct, pr—prostate cells, sg—shell gland, sr—seminal receptacle, ut—uterus, vd—yolk duct, ve—vasa efferentia, vgs—ventro-genital sinus, vr—yolk reservoir, vs—seminal vesicle.

PLATE 43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The cells of the shell gland are large and lie peripherally between the spaces of the vitellaria, from the level of the posterior margin of the ovary to about the anterior edge of the seminal receptacle. Their necks pass inward and surround the ootype for a short distance beyond the entrance of the yolk duct. These cells are not grouped in definite quadrants as in *A. varius.* The vitellaria arch over both dorsal and ventral surfaces in the region of the ovary. Anteriorly they are limited to the lateral regions.

The excretory bladder is Y-shaped, the pore terminal. The posterior stem is wide, but flatly compressed on the dorsal surface of the uterine coils. The testes lie dorsally, and in this region the excretory bladder is compressed between the testes and uterus. The bladder divides behind the ovary, and the anterior branches extend into the head region, internally to the crura, and dilate widely.

The terminal male apparatus is similar to that of *A. varius,* but lies completely posterior to the genital pore. It consists of a large folded seminal vesicle, separated from the terminal prostatic chamber by a narrow duct. The walls of the prostate portion contain the narrow papillose ends of the prostatic cells. These cells are pyriform, with long necks, and eccentric rounded nuclei. Their bodies lie peripherally.

The eggs of *A. artus* are provided with a curved point at the anopercular end, similar to the egg of *Cœcincola parvulus,* but have a smooth yellow shell. The point is homologous with the papilla of *A. varius,* but larger. The eggs are 0.017 mm. long by 0.013 mm. wide.

Allacanthochasmus varius Van Cleave, 1922

Plate 43, Figures 1–5

Spines cover the entire surface, but are slightly larger on the dorsal side. The vitellaria arch over the dorsal surface. The large seminal vesicle is mostly anterior to the acetabulum, and joins the genital cloaca on its anterior aspect. The uterus enters the common genital duct from the side. The common genital duct opens to the surface between the gonotyl and acetabulum.

The ovary is ventral. The oviduct emerges from the ovary at about the center of the cross section of the body, and connects with the dorsal seminal receptacle through the short amphiduct. Posterior to the amphiduct, Laurer's canal arises from the seminal receptacle and passes posteriad a short distance and opens to the surface in the mid-dorsal line. The typiduct arises from the amphiduct, reversing direction with the oviduct, and is shortly joined by the common yolk duct and merges into the ootype. The shell gland is peculiar in that its cells occupy a peripheral location in the quadrants of the body, beneath the sub-cuticula. Four groups of these cells occur in these areas, their long tubular necks extending radially inward to the ootype. The yolk reservoir lies centrally, with its two lateral ducts slanting back at an angle to meet it.

As a peculiar feature of this worm, the longitudinal muscles of the dermo-muscular sac are well differentiated into distinct small cords, which occupy a very regular parallel position beneath the cuticula.

The excretory bladder consists of a single median stem, of narrow, tubular form, extending forward dorsally to the mid region of the body. Here it branches laterally into two trunks, which pass anteriad and dilate greatly in the head region. The basal stem of the bladder is surrounded by folds of the uterus.

The genital cloaca passes inward between acetabulum and gonotyl to a distance about equal to one-third the depth of the body, and forks. The uterus passes posteriad. The male apparatus joins the duct anteriad, and the seminal vesicle and ejaculatory duct lie anterior to the acetabulum. The ejaculatory duct passes anteriad from the common genital duct, and is dilated to form a small chamber into which open the papillose ends of the prostate cells, giving its walls a spongy appearance. The prostate cells are peripheral, like those of the shell gland, and are very numerous, filling most of the parenchyma at this level. The prostate part of the male system joins the seminal vesicle by a short constricted curving duct. The nuclei of the prostatic cells are pyriform, and lie eccentrically with their tips in contact with the cell walls.

The egg is somewhat flattened on one side, on which, at the anopercular end, it bears a small terminal spine, homologous to the long spine of the egg of *A. artus,* here reduced to a vestige. The eggs are 0.023 mm. long by 0.013 mm. wide.

Discussion

The foregoing studies exclude the genus Vietosoma from the Heterophyidæ because of its dorsal ovary, cirrus sac, and lack of a seminal receptacle, and confirm previous conclusions to the effect that Acetodextra, Cryptogonimus, Cæcincola, Centrovarium, and Allacanthochasmus are related members of the Heterophyidæ. These heterophyids from fishes possess certain features in common. The ovary is ventral, and lobate. Laurer's canal is present and opens to the surface in the mid dorsal line, posterior to the ovarian complex. A seminal receptacle is present, anterior to the complex, usually near the dorsal surface. The amphiduct and Laurer's canal emerge from the seminal receptacle at approximately the same point. The typiduct reverses direction with the oviduct, passes ventrad a short distance, is joined by the yolk duct, and merges with the ootype. The neck of the uterus emerges from the ootype, crosses the anterior surface of the oviduct close to its origin from the ovary, and passes posteriad. The male system consists of a seminal vesicle, separated by a short duct from a prostatic chamber. The prostate cells have long necks, and their bodies are usually peripherally located. The prostatic portion of the duct is usually dilated into a small chamber with spongy walls formed by the papillose ends of the prostate cells.

Centrovarium offers an exception to this plan in that the amphiduct is greatly reduced, in consequence of which the oviduct, the entrance of the seminal receptacle, Laurer's canal, and the typiduct all come together at the same point, forming a four way system of ducts. The prostate cells and prostate portion of the male system are also reduced in this form. Nevertheless it appears that its affinities are with the Heterophyidæ, in spite of some degree of modification.

The eggs of *A. artus* and *C. parvulus* are similar in possessing a long spine opposite the operculum. On the other hand, the eggs of *C. parvulus* and *C. chyli* are similar in color and surface pattern. Because of conflicting characters it appears that the egg is of small value in indicating relationships.

The results of this study are in harmony with the relationships of certain fish heterophyids as suggested by Mueller and Van Cleave (1932) in their Plate 25. In this plate, however, the ovary of Cryptogonimus was inaccurately portrayed. A large series of mounts shows that the ovary in this form is usually follicular or multilobate, similar to the ovary of *A. artus*. On the other hand, the ovary of Cæcincola usually has three lobes instead of the four represented. Centrovarium, lacking a gonotyl, is undoubtedly a large aberrant form which belongs somewhere near Cæcincola. It further appears probable that the genera Cryptogonimus, Acetodextra, and the mammalian genus Heterophyes represent an evolutionary series.

Between the subfamilies Heterophyinæ and Neochasminæ the chief difference in internal organization is the position of the shell gland. In the genus Allacanthochasmus (Neochasminæ) the cells of the shell gland are peripherally located, which may be a subfamily characteristic, whereas, in the genera Centrovarium, Cæcincola, Cryptogonimus, and Acetodextra (Heterophyinæ), the cells of the shell gland are central in position. In both subfamilies the prostatic cells tend toward a peripheral position.

Conclusions

1. Vietosoma is excluded from the Heterophyidæ, since it lacks a seminal receptacle and possesses a cirrus sac.

2. The genera Acetodextra, Cæcincola, Cryptogonimus, Centrovarium, and Allacanthochasmus agree in anatomical plan, and are correctly placed under the Heterophyidæ.

3. The circumoral spines, and differences in position of the shell gland, in the genus Allacanthochasmus indicate that the separation of the Neochasminæ from the Heterophyinæ is valid.

Bibliography

References cited in this article will be found in the bibliography at the end of Part III.

SECTION 2. FURTHER STUDIES ON CERTAIN SPECIES OF TREMATODES FROM ONEIDA LAKE FISHES

In parts I and II of this series of papers many of the new species were described on the basis of their gross anatomy only, lack of time, and in some cases lack of material, preventing a detailed study. In order to supply further information on these forms the present author has undertaken to restudy them in detail. Certain of these results appear in the preceding section on the Heterophyidæ. The progress of the study has been dependent upon the acquisition of additional material in the case of species where only a few specimens had been taken, and these previously mounted for study as toto mounts. Those species of which material could be had for sectioning are described below. As soon as additional material of the other species becomes available they also will receive detailed study.

Family Allocreadiidae

Triganodistomum attenuatum Mueller and Van Cleave, 1932

Plate 44, Figures 1–6

The oviduct ascends from the right side of the ovary, passes forward a short distance and to the center of the body where it at once branches three ways. The branch immediately opposite the oviduct is Laurer's canal. This makes a sigmoid curve, and opens on the dorsal surface in the mid line. It lies throughout in the same horizontal plane. A second branch forms the entrance of the seminal receptacle which in this species is small, but clearly defined. In four series of sections of worms of various sizes it uniformly failed to contain sperms. The receptaculum lies in a dorsal position. Opposite its opening the typiduct continues ventrad, traversing the body of the worm in the same horizontal plane, and passing close to the ventral surface, where it bends sharply anteriad. At this bend it is joined by the common yolk duct, ascending from the rear, and immediately anterior to this point occurs the ootype, surrounded by Mehlis's gland. The cells of the gland occupy most of the space between the crura at this level. The ootype continues into the uterus. The uterus coils several times, anterior to the ootype, finally crossing over and descending on the left side to the caudal region. Here it loops, ascends forwardly again, anterior to the ootype, and descends to the caudal region, where it performs several loops, ascends again on the right side to the post acetabular region, and crosses over to the genital pore. It opens in the common genital pore just posterior to the cirrus. In the original description the uterus of this species was incorrectly described and figured, in that it was represented that the terminal sling of the uterus ascended on the left side, and to the pore. Sections show that the uterus passes to the pore, across the body from the right side. The ovary has three chief lobes, but these are somewhat subdivided superficially into smaller prominences.

The seminal vesicle is divided by a median partition. The prostatic cells are well developed. The inverted cirrus has a thick, muscular wall. The vasa efferentia pass anteriad, laterally on the ventral surface, pass dorsad, laterally to the ootype, and swinging to a central position unite just before entering the seminal vesicle.

The excretory pore is subterminal on the dorsal surface. The excretory bladder is long, narrow and tubular, dorsal to the testes. At about the middle of the anterior testis it branches into two lateral tubules, which sweep around the testis, and pass to the ventral surface near the ovary. From here on these tubules have a divided lumen, so that in cross section they appear like a figure eight. They pass anteriad on the ventral surface of the crura to the level of the seminal receptacle and the genital pore. The left tubule passes dorsal to the cirrus pouch. In the acetabular region the tubules lie lateral to the crura, and proceeding to the head region they converge, loop several times at the level of the pharynx, and disappear. A number of secondary tubules, also with divided lumen, are given off throughout the course.

The dorsal surface of the worm is covered with a smooth cuticula devoid of spines. This cuticula stains differently from that of the ventral surface, being basophilic in reaction. Beneath this surface is a conspicuous layer of irregular

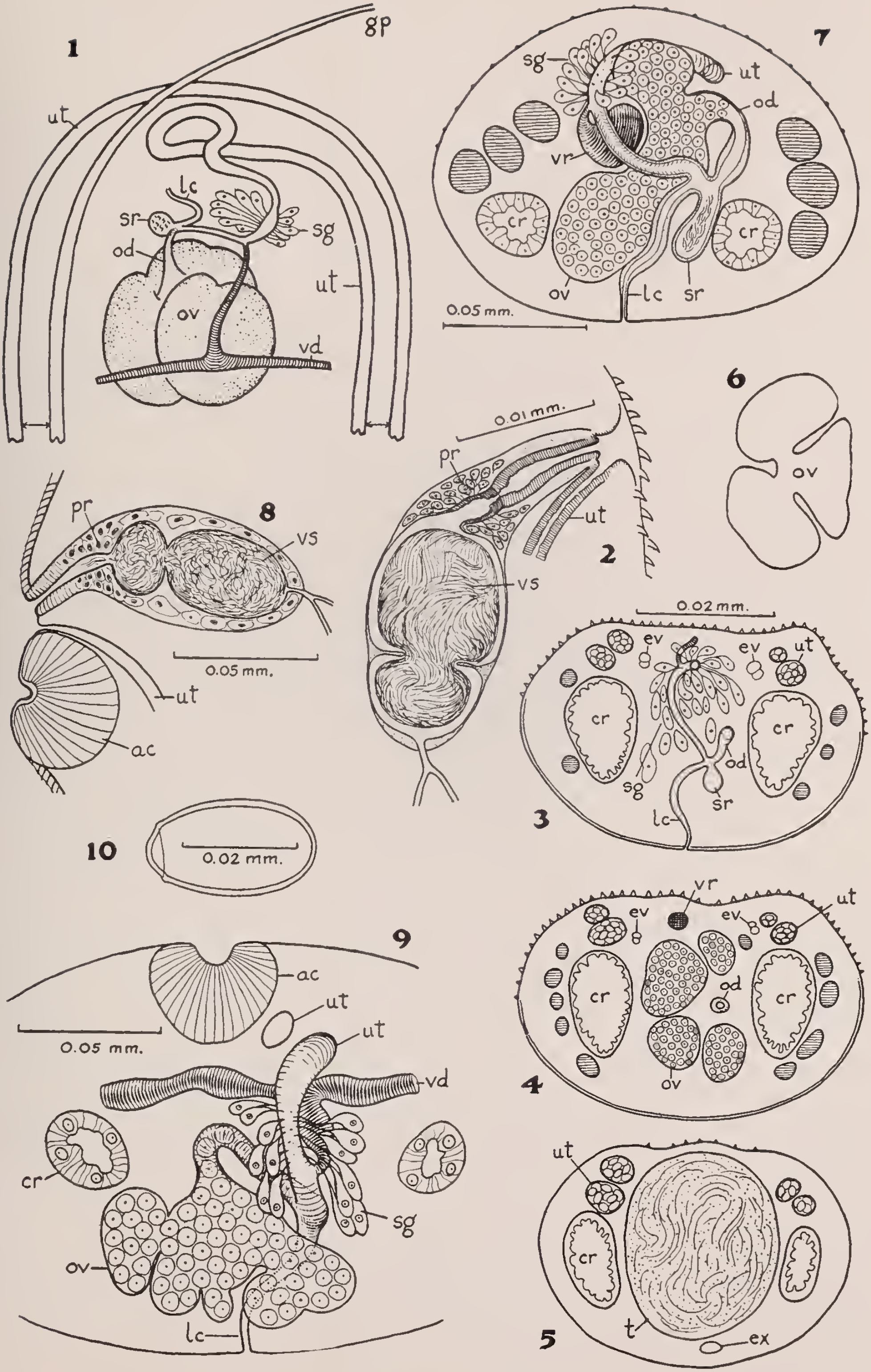
Plate 44. *Triganodistomum attenuatum.* 1, Diagram of female genitalia, seen from ventral side, showing path of uterus. 2, Cirrus sac and genital pore. 3, Cross section composite of female genitalia. 4, Cross section immediately posterior to figure 3, showing origin of oviduct. 5, Cross section through posterior testis. 6, Cross section of ovary at mid level (posterior to Fig. 4), showing three main lobes.

Triganodistomum simeri. 7, Composite cross section of female genitalia, anterior view.

Vietosoma parvum. 8, Cirrus sac and genital pore. 9, Composite cross section of female genitalia, anterior view. 10, Egg.

ac—acetabulum, cr—crura, ev—excretory vessel, ex—excretory bladder, gp—genital pore, lc—Laurer's canal, od—oviduct, ov—ovary, pr—prostate, sg—shell gland, sr—seminal receptacle, t—testes, ut—uterus, vd—yolk duct, vr—yolk reservoir, vs—seminal vesicle.

PLATE 44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glandular cells, their ducts opening to the surface, and their granular cytoplasm also taking on nuclear stains. These cells are less apparent on the ventral surface. Spines appear at the dorso-lateral angle, and continue over the ventral surface, being best developed in the mid ventral region. Around the oral sucker they appear for a short distance on the dorsal surface. Posteriorly they become completely restricted to the ventral surface, and finally disappear posterior to the second testis.

Triganodistomum simeri Mueller and Van Cleave, 1932

Plate 44, Figure 7

The ovary occupies most of the intercrural region at its level, from the ventral to the dorsal surface, and the oviduct emerges on the right side of the ovary near its ventral margin, curves anteriad and dorsad along the side of the ovary, and passes to the seminal receptacle. At the point of junction arises a fork, one branch of which, Laurer's canal, passes in a sigmoidal curve and opens on the mid line of the dorsal surface. The ventral branch (the typiduct) passes over the anterior surface of the ovary to the left side and is joined by the yolk duct, and passes into the ootype surrounded by the shell gland. The uterus continues posteriad along the ventral surface. The cells of the shell gland form a compact cluster anterior to the yolk reservoir near the ventral surface. The transverse yolk ducts lie ventral to the crura.

The excretory pore is terminal and the excretory bladder tubular, consisting of a narrow vessel only one-half the diameter of the crura, passing anteriad along the dorsal surface to the level of the middle of the anterior testis. Just short of its tip it branches into two ducts passing ventrad, internal to the crura, and these continue forward, but cannot be followed beyond the ovary.

The cirrus sac, though smaller, is similar to that of *T. attenuatum*. It consists of a bipartite seminal vesicle, a well developed prostatic portion, and the muscular cirrus. The metraterm enters the genital pore posterior to the cirrus.

There is considerable variation in the details of different specimens, doubtless due to the tight crowding of the organs within the body. In this respect this species forms a contrast with *T. attenuatum,* where the plan of arrangement is in all specimens quite uniform, and where there is a large amount of space between the organs. Small spines occur on the ventral surface; the dorsal surface is smooth.

Like *T. attenuatum, T. simeri* also violates Simer's definition of the genus in that a seminal receptacle is present. Though small, this organ contains sperms, whereas in *attenuatum* it was found to be empty. An additional point of agreement between the two species is found in the limitation of spines to the ventral surface, though in *simeri* they are very much smaller than the large rugged spines of *attenuatum*. The eggs of *simeri* are thin shelled, elliptical, 0.0238 mm. long, by 0.011 mm. wide.

Discussion

Simer created the genus Triganodistomum for a single species, *T. translucens*. In the light of additional information it appears that in certain respects the generic diagnosis must be emended. Simer states that no seminal receptacle is present. In

T. attenuatum the seminal receptacle is present, but vestigial, and apparently non-functional, while in *T. simeri* the seminal receptacle is present, and though small, contains sperms.

Genus Triganodistomum, char. emend.

GENERIC DIAGNOSIS: Small Allocreadiidæ elongate with tapering or rounded ends, and oval or circular in cross section. Suckers large, anterior smaller than posterior. Prepharynx short or absent, esophagus short. Ceca pass posterior testis. Testes two, globular, linear, in posterior body region. Cirrus sac crescentic, with seminal vesicle, prostate, and protrusible cirrus. Genital pore sinistral, near middle of acetabulum. Ovary with three distinct lobes, at anterior border of first testis. Receptaculum seminis vestigial, or absent (?). Uterus well filled with small eggs, and looping into posterior region of body. Vitellaria of small follicles, lateral, from level of ventral sucker to posterior testis.

Plagiocirrus primus Van Cleave and Mueller, 1932

Plate 45, Figures 2–6

The cuticula is smooth, and spineless. The ovary lies toward the right, and the oviduct emerges from the posterior face of the ovary, passes centrally, and branches three ways. The branch opposite the oviduct is Laurer's canal, and passes, with some coiling, to the dorsal surface, on which it opens to the left of the mid line. The right branch forms the opening of the seminal receptacle, which is small, and apparently non-functional. It is directed posteriad. The remaining (left) branch coils and passes ventrad, bends posteriad, and is joined by the yolk duct. It then expands to become the ootype, and is surrounded by the shell gland. The cells of Mehlis' gland form a small ventral cluster posterior to the ovary. The uterus thence passes posteriad. The yolk reservoir lies dorsally, its common duct is long, and traverses the dorso-ventral diameter of the body to join the ootype. The transverse yolk ducts pass laterad in an arc, internal to the crura. The ovarian complex is somewhat strung out longitudinally, instead of being grouped in approximately the same transverse plane.

The genital pore lies at the left ventro-lateral angle of the body. The cirrus sac passes inward diagonally and lies centrally above the acetabulum. The terminal muscular portion is poorly developed, and whether the tip is eversible is doubtful. The prostate cells are numerous. The ejaculatory duct makes a half-coil before joining the seminal vesicle, which is simple and undivided.

The excretory bladder is narrow, and tubular, and passes anteriad on the dorsal surface of the testes to a short distance posterior to the ovary. Short of its anterior extremity it gives rise to two lateral ducts which pass anteriad, and for a part of their course have a divided lumen, such as occurs in Triganodistomum.

Relationships with this latter genus are indicated by the position of the genital pore, reduction of the seminal receptacle, and character of the excretory canals. Differences are apparent, however, in the smooth cuticula, the structure of the cirrus sac, the undivided ovary, and the position of the external opening of Laurer's canal, which is on the mid line in Triganodistomum.

Plate 45. Allocreadiidae.

Allocreadium lobatum. 1, Ventral view of cleared whole mount.

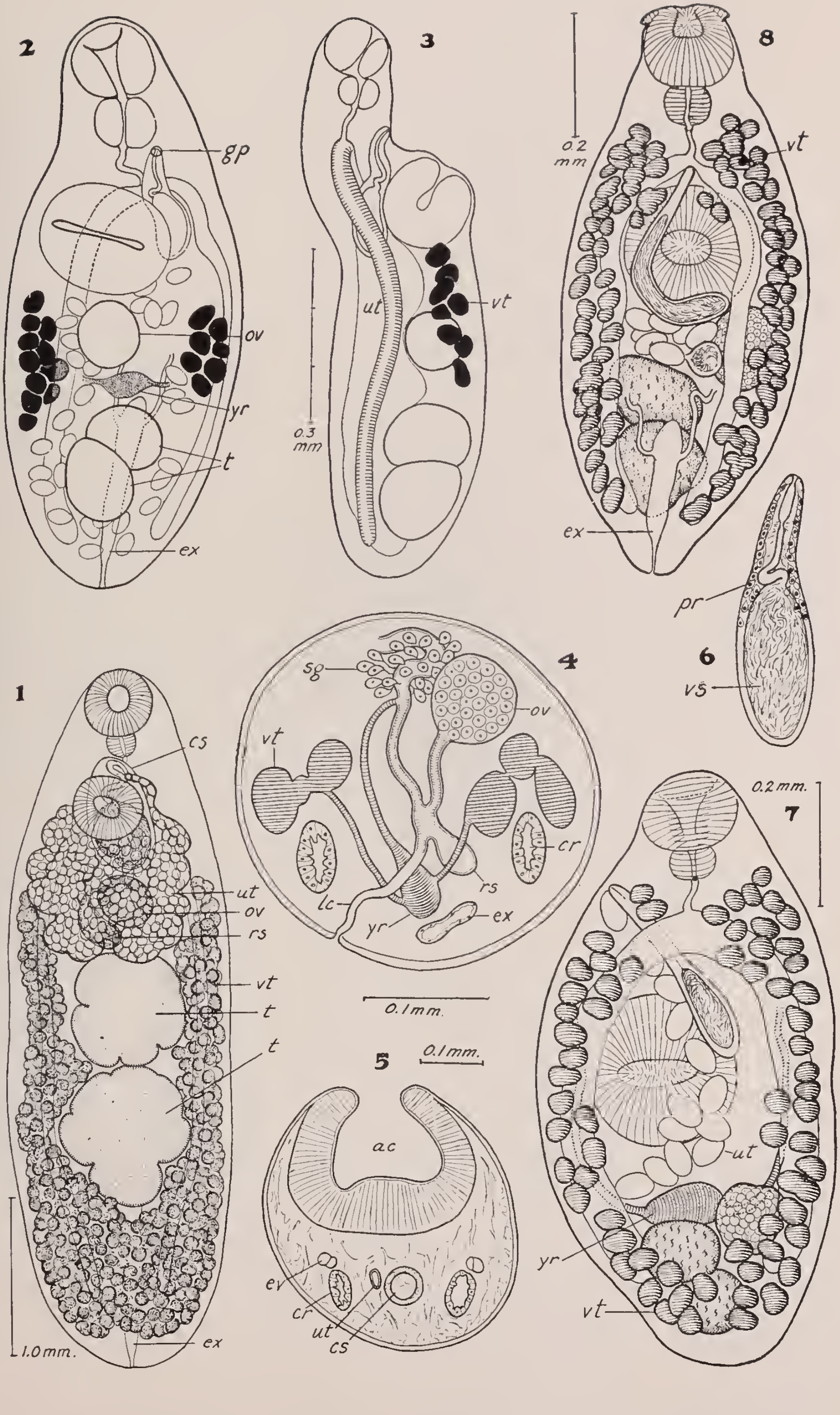
Plagiocirrus primus. 2, 3, Ventral and lateral views of cleared whole mounts. 4, Cross section composite of female genitalia, anterior view. 5, Transverse section through acetabulum. 6, Cirrus sac.

Plagioporus sinitsini. 7, Dorsal view of the whole worm.

Creptotrema funduli. 8, Dorsal view of whole worm.

ac—acetabulum, cr—crura, cs—cirrus sac, ev—excretory vessel, ex—excretory bladder, gp—genital pore, lc—Laurer's canal, ov—ovary, rs—seminal receptacle, sg—shell gland, t—testes, ut—uterus, vs—seminal vesicle, vt—vitellaria, yr—yolk reservoir.

PLATE 45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SECTION 3. ADDITIONAL SPECIES OF PARASITES FROM ONEIDA LAKE FISHES

During further studies on the lake and its closely adjoining tributary waters subsequent to completion of work on Part III, a number of additional species of parasites were encountered and for the sake of convenience and completeness these are treated below. Certain of these species are not new, but hitherto they have not been found in Oneida Lake. Others constitute further additions to the already considerable list of new species here found.

Family Allocreadiidae

Allocreadium lobatum Wallin, 1909

Hosts.—*Leucosomus corporalis, Semotilus atromaculatus;* in intestine.

Plate 45, Figure 1

This trematode was found during the summer of 1933. One specimen was taken from a Semotilus, and three were taken from two individuals of Leucosomus.

A study of this material from toto mounts and sections shows it to be the same as Wallin's species. The worms range from 2 mm. to 4 mm. in length. Thus these specimens were a little smaller than those of Wallin, who gives 3 mm. to 6.7 mm. as the length of his specimens.

The cuticula is smooth, the suckers about equal in size and located in the anterior fourth of the body. The uterus is confined to the second quarter. The ovary lies dorsal to the uterus, obscured by its folds, and the lobate testes lie serially, the anterior testis in about the middle of the body, the posterior close behind it. The vitellaria extend from the level of the ovary in the lateral fields back to the caudal extremity, meeting in a wide band posterior to the testes. The excretory bladder passes forward dorsally from the terminal pore, and ends a little anterior to the posterior margin of the posterior testis.

The genital pore lies on the anterior margin of the acetabulum. Wallin's specimens seem to have been more expanded in the anterior region, as he shows the genital pore and fork of the crura a short distance anterior to the acetabulum. The cirrus sac in my specimens is like that figured by Wallin for *lobatum,* with a folded, voluminous seminal vesicle, and a crooked ejaculatory duct surrounded by a pars prostatica. The relative size of the cirrus sac varies. In the larger specimens it reaches beyond the acetabulum, while in a small worm from Semotilus the cirrus sac is almost entirely anterior to the acetabulum. Also, in my material the fork of the intestine lies dorsal to the acetabulum, whereas Wallin shows it as anterior. Nevertheless, it is quite certain that this material is *lobatum,* for the ootype and other morphological details correspond to Wallin's figures. Laurer's canal and a large seminal receptacle are present.

The worms in life are salmon pink, and slow in movement. Wallin's material had been collected by Professor H. B. Ward from the stomach of *Semotilus bullaris* in Sebago Lake, Maine. Pearse, 1924, found this species in the intestine of *Catostomus commersonii* in Wisconsin. The present record extends the host list to *Semotilus atromaculatus* and *Leucosomus corporalis* from Oneida Lake.

Plagioporus sinitsini Mueller, 1934

Plate 45, Figure 7

Synonym: *Allocreadium commune* Cooper, 1915, in part.

Host.—*Catostomus commersonnii,* fingerling, in gall bladder.

This worm was described elsewhere (Mueller, 1934). Only two specimens have been found despite extended search. The genital pore is on the left side at the pharyngeal level, and the long cirrus sac extends back and overlaps the anterior portion of the acetabulum, in which character it was necessary to emend the definition of the genus Plagioporus as given by Sinitsin. The gonads lie at the posterior end of the body, the ovary forward, and the uterus consists of several small loops anterior to the ovary, passing to the genital pore.

A single small sucker, with two of these worms in its gall bladder, was taken in a small shoreline indentation on the south side of the lake, near Brewerton, May 10, 1933.

Creptotrema funduli Mueller, 1934

Plate 45, Figure 8

Synonym: *Allocreadium commune* Cooper, 1915, in part.

Host.—*Fundulus diaphanus menona,* in intestine.

This has been described with the preceding species (Mueller, 1934). The worm is one of the papillose allocreads, but differs from the related genus Crepidostomum in having only the two lateral papillæ on the oral sucker. These papillæ are greatly reduced and escape detection unless searched for very carefully. This species was the second member of the genus to be reported, and the first member of the genus for North America.

Fundulus specimens from Oneida Lake bear a very heavy infestation with these worms, frequently having as many as fifty in the intestine. Their usual location is the upper part of the intestine.

Family Azygiidae

Proterometra macrostoma (Faust, 1918)

Dickermann has recently reported on the anatomy and life history of a cystocercous cercaria of the Mirabilis group, from *Goniobasis livescens* in the Des Plaines River, Ill. This form was first described as *Cercaria macrostoma* Faust, 1918, but Horsfall, 1933, made the new genus Proterometra to receive it. The cercaria has a large yellow tail with a pair of flippers at the end. The distome is at first attached to the end of the tail, but upon escape from the snail crawls inside the proximal end of the tail. Pratt, 1919, recorded from *Goniobasis livescens* from the Oneida River *Cercaria fusca,* which is a cercaria of this same type. Because of discrepancies in Pratt's description Dickermann hesitated to synonymize *C. fusca* with *C. macrostoma.* I have examined Pratt's material of this form, and although I have not given it detailed study, it is obvious that it is the same form as *C. macrostoma.* I am therefore reporting, on the basis of Pratt's material, *Proterometra macrostoma* from Oneida Lake. The adult worm lives in the esophagus of the sunfish, bluegill, and crappie. We have not taken in our own collecting either the adult from the fish, or the larval forms from the snail.

Monogenea (Ectoparasitic Trematodes)

Octomacrum lanceatum n.g. and n. sp.

Plate 46, Figures 1–9

Synonym: *Octobothrium sagittatum*, Wright, 1879.

Host.—*Catostomus commersonnii*, and *Erimyzon sucetta oblongus*, on gills.

This worm was found rather commonly on gills of suckers from an artificial widening of Frederick Creek forming the reservoir of the State Fish Hatchery at Constantia. Both the chub sucker and the common sucker carried these worms, the parasite apparently thriving equally well on both. Suckers from Oneida Lake proper, just a short distance away, or from other tributaries, have not been found to carry the worm. In all probability this is the same species that was reported by Wright (1879) under the name of *Octobothrium sagittatum*, from the gills of *Catostomus teres*. Although Wright notes that the habitat of his material was uncertain, it is to be presumed that it was of Canadian origin, and probably from some locality in the Toronto region. A study of this material shows that it is not *Octobothrium sagittatum* of Leuckart or Olsson, from which it differs in many critical characters. *O. sagittatum* is a European species found on the gills of salmonids and probably does not occur on this continent. Recent authors include Octobothrium under the genus Discocotyle Diesing.

Shaffer (1916) described *Discocotyle salmonis* from the gills of rainbow trout from New York State fish hatcheries. My material from suckers differs not only from *D. salmonis* but from all other previously described species and constitutes a new genus.

Octomacrum, n. g.

Generic diagnosis: Octocotylidæ. Body tapering to a point anteriorly. Cotylophore with eight small sessile suckers arranged in two lateral rows of four each. No hooks on posterior margin of cotylophore. Vagina lacking, genito-intestinal canal present. Type species: *Octomacrum lanceatum*.

This genus in general resembles Discocotyle (Octobothrium), but differs in lacking the vagina, which in Discocotyle is present and Y-shaped. It differs from Macrozæs and Octocotyle in lacking the vagina and in the absence of small posterior hooks on the sucking disc. It differs from Dactylocotyle and Diclidophora in that the posterior suckers are not stalked.

Octomacrum lanceatum n. sp.

Worms 5 mm. to 6 mm. long by 1.5 mm. to 2 mm. wide. Cotylophore rectangular and set off from rest of body by a slight constriction. Suckers large, with their edges in contact, decreasing in size posteriorly. Anterior suckers 0.340 mm. wide by 0.270 mm. long. Entire cotylophore 0.685 mm. wide and about 0.800 mm. long. The suckers are provided with a chitinous framework, more complicated than that described by Shaffer for *D. salmonis*, but essentially similar to that of *D. sagittatum*.

The mouth is at the anterior tip of the body. The dorsal lip has the character of a muscular papilla. Within the oral cavity are two lateral suckers having a maximum diameter of 0.1 mm. The pharynx, just posterior to these, is somewhat smaller. The intestine is Y-shaped and with many transverse branches, but these do not anastomose, nor do the crura join at the posterior end. The crura terminate at the same level and do not extend into the cotylophore. In living worms the intestine is filled with blood of the host and with the contractions of the worm the intestinal contents are constantly swept from one crus into the other. The ovary lies about mid way on the right. It is a long cylindrical organ but crowded to form a compact coil. The yolk reservoir is ventral, anterior to the ovary. The oviduct is ciliated and a short distance from the ovary branches two ways. One branch passes to the right crus and forms the genito-intestinal (Laurer's) canal. The internal wall of this canal is thrown into numerous folds which probably serve as valves to prevent backwash from the intestine into the ootype. That this canal is actually functional was proved by finding masses of spermatozoa in the intestinal branches near the point of entrance. The other branch from the oviduct is joined after a short distance by the yolk duct, and thence continues dorsally through the mass of the shell gland. At its point of emergence from the shell gland it is surrounded by a sphincter muscle, which marks the lower end of the uterus. The uterus consists of two parts. The posterior part is a chamber lined with an unciliated epithelium, with large nuclei. Gland cells lying removed in the parenchyma send their long necks inward to empty into this chamber. The anterior portion of the uterus is a muscular tube containing ciliated walls. This tube opens to the surface ventrally at the genital pore. Just posterior to the genital sucker it dilates into a small chamber. No eggs were found in any of my worms, but the egg of presumably this same species has been figured by Wright as having a plump oval body and very long filament. The vitellaria are very numerous and fill in all of the parenchymal space not occupied by other organs.

The testis is a multilobate body lying posterior to the ovary. The vas deferens ascends dorsally to the genital pore. Here it terminates in a hollow chitinous cirrus, surrounded by the genital sucker. No genital hooks are present. The cirrus and its associated structures are different from any arrangement which I have been able to find in the descriptions of related worms. The cirrus is about 0.05 mm. long, tubular at the base, but cut away on one side toward the tip to form a long, sharp point. It is traversed by the vas deferens and doubtless serves as a true intromittent organ.

The genital pore lies at the level of the intestinal fork. The genital sucker is spherical in outline but its cavity is drawn out into four grooves, anterior and posterior, and two lateral, separated by bulges of the muscular wall. The cirrus perforates the dorsal wall of the sucker. The uterus appears to open to the exterior ventral to the genital sucker.

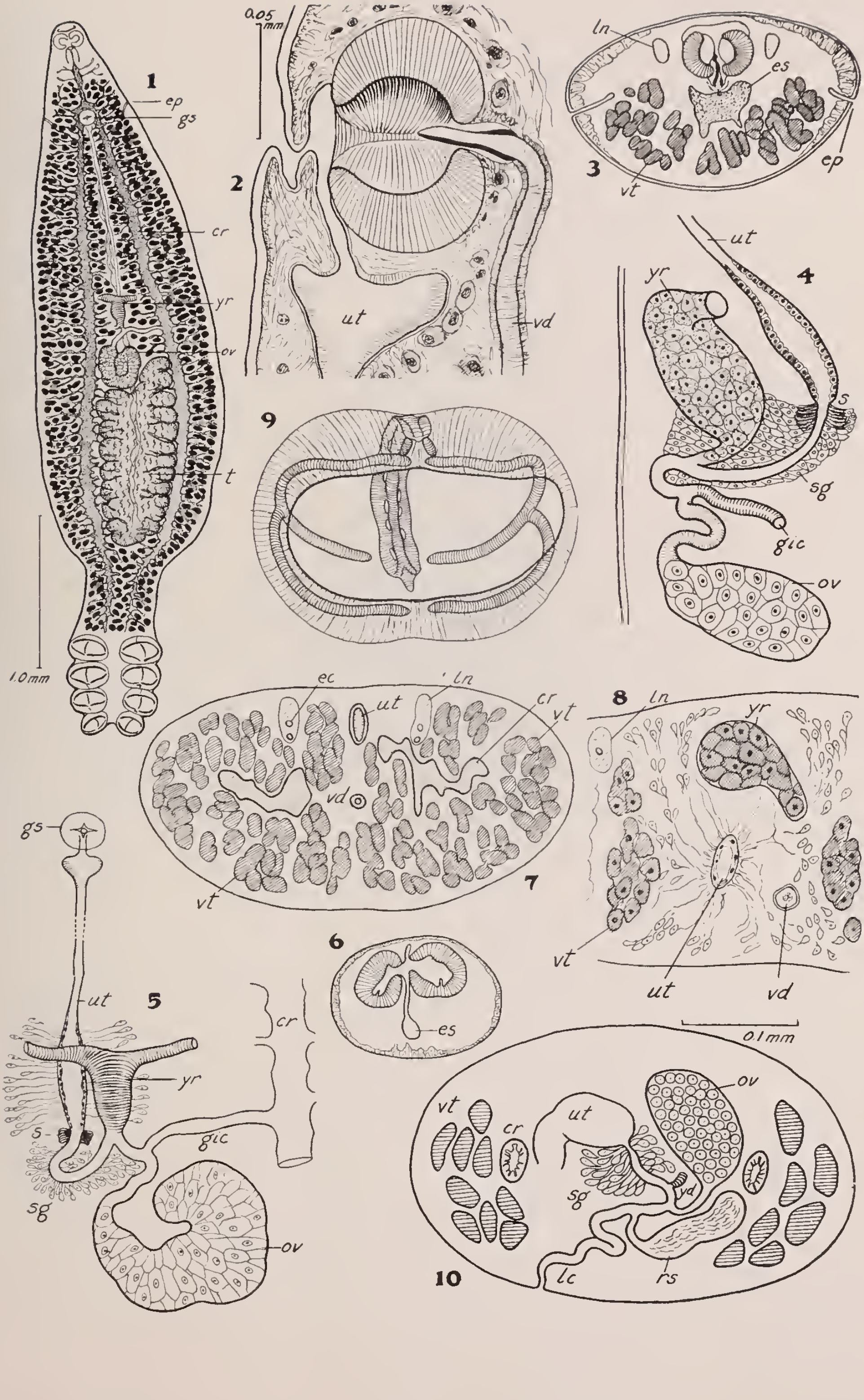
The nervous system consists of a ganglion in the region of the intestinal fork and lateral trunks passing posteriad on the ventral surface. The excretory system has two pores opening on the lateral margin at the level of the genital pore. The excretory ducts traverse the length of the body close to or encased in the nerve trunks. At the region of the excretory pores the ducts diverge toward the margin at a 45-degree angle.

Plate 46. *Octomacrum lanceatum.* 1, Ventral view of whole mount. 2, Sagittal section through genital pore showing interior of genital sucker and chitinous cirrus. 3, Transverse section at level of genital pore. 4, Composite of sagittal sections showing relationships of female genitalia. 5, Diagram of female genitalia in ventral view. 6, Transverse section through level of lateral oral suckers. 7, Transverse section through anterior third of body between genital pore and yolk reservoir. 8, Transverse section, detail, through yolk reservoir showing uterine glands. 9, One of the caudal suckers showing the chitinous framework.

Anallocreadium pearsei. 10, Transverse section composite, anterior view, showing relationship of female genitalia.

cr—crura, ec—excretory canal, es—esophagus, ep—excretory pore, gic—genito-intestinal canal, gs—genital sucker, lc—Laurer's canal, ln—longitudinal nerve trunk, ov—ovary, rs—seminal receptacle, s—sphincter muscle, sg—shell gland, t—testes, ut—uterus, vd—vas deferens, vt—vitellaria, yd—yolk duct, yr—yolk reservoir.

PLATE 46


1
ep
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ln
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ut
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lc
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This is doubtless a native American species. Whereas most of the Octocotylidæ and Monogenea in general are very specific in their host relations, this form is of interest in that it appears to adapt itself to two host species, on either of which it thrives equally well.

Cotypes of this species have been deposited in the collections of the U. S. National Museum, No. 32570.

Gyrodactylidae, Tetraonchinae

The literature on the Gyrodactylidæ has been reviewed in previous parts of this study and a number of forms have been described from the Oneida Lake fishes, most of them new species. The present author is continuing work on the native members of this group, with the result that several additional new species have been found to date from the Oneida Lake area, and are set forth below.

Although numerous genera of the Tetraonchinæ have been described, chiefly from Europe, Japan and Australia, and a number on the basis of McCallum's work on the parasites of our native marine fishes, a number of the fresh water forms of North America do not fit into any of the established genera, so that new ones must be established for their reception.

Cleidodiscus n. g.

Diagnosis.—Tetraonchinæ, with intestine bifurcated, but confluent posteriorly. Ovary and testis near center of body; vagina present, with large seminal receptacle. Cirrus with two chitinous points. Vitellaria from pharynx to posterior margin of intestine. Caudal disc flat, with four large hooks, and twelve small hooklets. Four eyes present. Type species: *Cleidodiscus robustus,* n. sp.

This genus stands near Empleurosoma and Daitreosoma, but is distinctly different from these in that the yolk glands extend into the posterior third of the body, and the disc has 12, instead of 2, small marginal hooklets.

Cleidodiscus robustus, n. sp.

Plate 47, Figures 1–4

Host.—*Eupomotis gibbosus,* on gills.

Stout worms about 0.945 mm. long by 0.231 mm. wide, with relatively small attachment organ poorly set off from rest of body. Attachment organ somewhat rectangular, about 0.115 mm. wide by 0.062 mm. long. The four main hooks relatively small, compared with those of other worms, with a strongly curved extremity and a simple flat shaft, greatest dimension about 0.023 mm. Marginal hooklets 12 in number, with tubular shafts, grouped two on each dorso-lateral angle, three on each ventro-lateral angle, and two toward the ventral edge between the main hooks. Longitudinal muscle strands pass through the caudal peduncle into the disc and expand into club shaped extremities attached to the hooks. These extremities are surrounded by conspicuous empty spaces. The four main hooks are nearly equal in size, but the two dorsal appear to be slightly smaller than the ventral.

The intestinal trunks join about three-fourths of the length back in the body. The vagina lies on the left margin about one-third the length back from the head, and at this level there is a slight constriction. The vagina is short, leading into a spacious seminal receptacle. The oviduct joins the duct from the seminal receptacle and is then surrounded by the shell gland to form the ootype. Thence the short uterus proceeds to the genital pore which lies at the level of the intestinal bifurcation. The testis is a saccular body, the anterior half of which is crowded with sperms. The vas deferens curves sharply to the left, passes over the vagina dorsally, recurves to the right and is thrown into a number of dilated coils constituting the seminal vesicle, which terminates in the cirrus. The chitinous cirrus is 0.054 mm. long. The pharynx has a maximum diameter of 0.047 mm. The eye spots are comparatively small, the anterior smaller than the posterior, and slightly closer together. A large group of cells of the cephalic glands appears to either side of the pharynx.

The egg is provided with a polar filament. Exclusive of the filament it is 0.069 mm. long by 0.046 mm. wide. The filament is about 0.1 mm. in length.

This worm was found on the gills of sunfish from the State Fish Hatchery reservoir at Constantia, N. Y., about one-half mile north of Oneida Lake, where it occurred in multiple infestations with two other species described below. Cotypes are in the collections of the Roosevelt Station.

Cleidodiscus fusiformis n. sp.

Plate 47, Figures 10–11

Host.—*Micropterus dolomieu,* on gills.

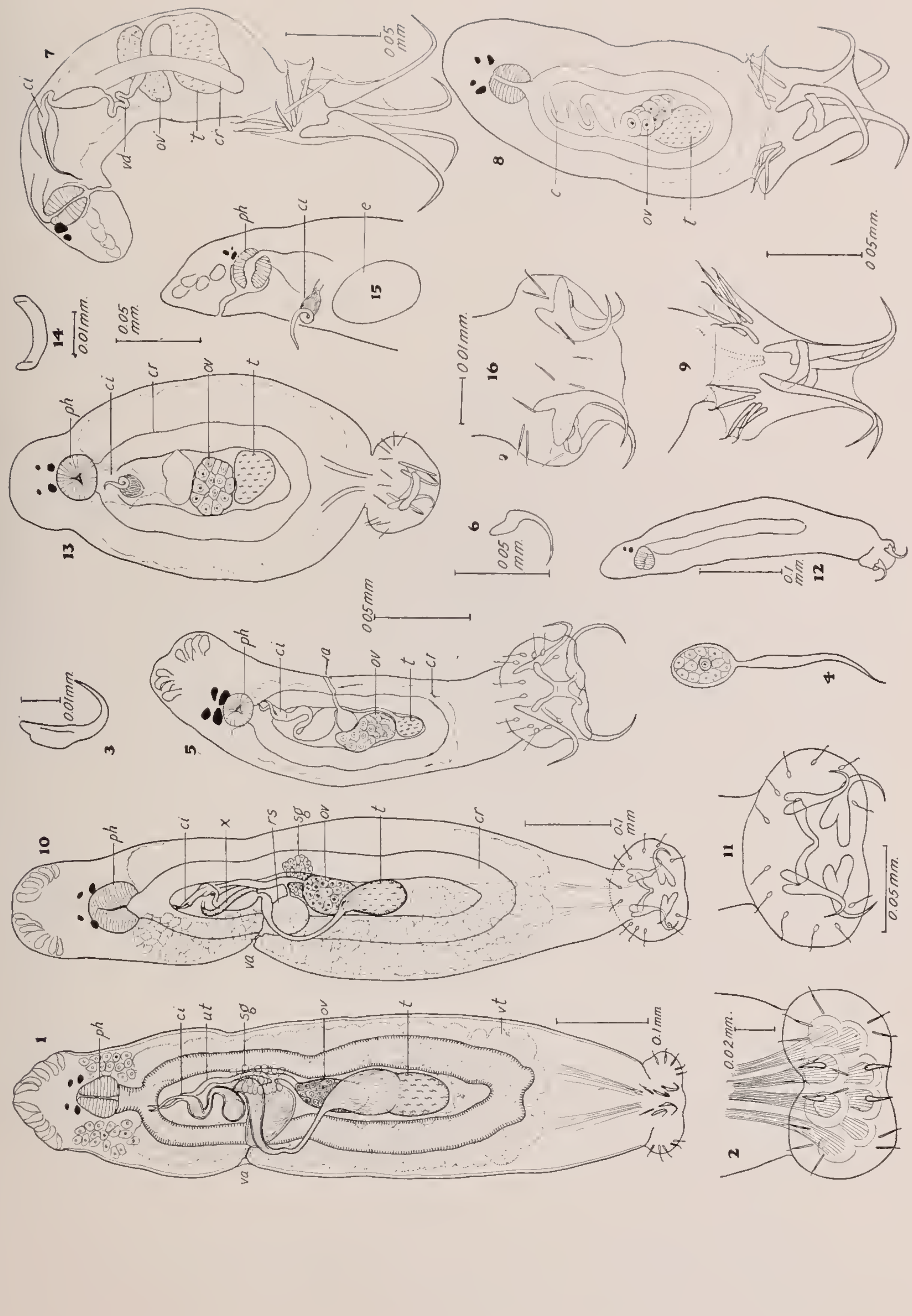
Somewhat tapering worms, 0.550 mm. to 0.850 mm. in length, and about 0.170 mm. in greatest width. Attachment organ rounded, about 0.096 mm. in diameter, well set off from the caudal peduncle. The four main hooks are of approximately the same size and shape, with a strongly curved exposed hook, and a broad, bifid shaft embedded in the disc. The greatest dimension of a hook, not following the curve, is 0.044 mm. The width of the shaft at the broadest point is 0.0136 mm. The two ventral hooks articulate with a V-shaped clamp, with expanded ends. The dorsal pair, however, appears to lie free in the disc, without any articulating support. The two rami of the shaft are nearly equal in length in the ventral hooks, but unequal in the dorsal. Around the edge of the disc are located twelve small hooklets, each with a small rounded base lying in the muscles of the disc, a slender shaft leading to the surface, and a curved exposed point. These hooklets are grouped two on the ventral edge between the main hooks, a group of three on each antero-lateral margin of the disc, and a pair on each postero-lateral margin. The disc is deflected toward the ventral surface so that the dorsal edge and hooks appear posterior.

The pharynx is 0.065 mm. in greatest diameter. The intestine forks and becomes confluent again at the level between the third and fourth quarters of the body. The vagina lies on the left margin, about one-third the length from the head, and leads into a spacious seminal receptacle. This by a short duct communicates with the oviduct. The ovary lies near the center of the body, and the oviduct passes forward on the right. Near the connection with the seminal receptacle the tube is surrounded by a small shell gland.

Plate 47. Cleidodiscus and Urocleidus. 1, *C. robustus* from sunfish, dorsal view. 2, Ventral view of tail. 3, One of the main hooks. 4, Egg. 5, *C. oculatus* from sunfish, ventral view. 6, One of the main hooks. 7, 8, *U. ferox* from sunfish, lateral and ventral views. 9, Ventral view of tail. 10, *C. fusiformis* from *M. dolomieu*. 11, Tail, ventral view. 12, *U. angularis,* from Fundulus, lateral view of an elongate specimen. 13, Ventral view of a contracted specimen. 14, One of the chitinous clamps. 15, Lateral view of head, showing egg and cirrus. 16, Lateral view of attachment organ.

ci—cirrus, cr—crura, e—egg, ph—pharynx, rs—seminal receptacle, sg—shell gland, t—testis, ut—uterus, va—vagina, vd—yolk duct, vt—vitellaria, x—rod-shaped body of unknown function.

PLATE 47


1
ph
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3
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a
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4
13
6
0.05 mm.
12
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14
0.01mm.
0.05 mm.
15
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0.05 mm
8
c
0.05mm.

The testis partly overlaps the ovary dorsally, and the vas deferens passes sharply to the left, curves dorsally over the vagina, and mediad again, where it dilates into several compartments to form the seminal vesicle. The cirrus has a muscular base and chitinous extremity consisting of a tube terminating in two slightly twisted points. Lying dorsally, above the seminal vesicle, curving from left to right, is a yellowish, spindle-shaped rod, of a homogeneous, finely granular character (x, Plate 47, Figure 10). This organ stained deeply in eosin, but its function or connections could not be discovered. The vitellaria extend continuously from the pharynx to near the caudal peduncle.

The eye spots are four, the anterior pair smaller and closer together than the posterior.

This worm was found in small numbers on the gills of the small mouth bass from the State Hatchery reservoir at Constantia. Cotypes are in the collection of the Roosevelt Station.

Cleidodiscus oculatus n. sp.

Plate 47, Figure 5

Host.—*Eupomotis gibbosus,* on gills.

A smaller form, and studied only from whole mounts. Length about 0.240 mm., width 0.054 mm. The caudal disc provided with four large hooks, approximately similar in shape, and arranged much as in the preceding species. Greatest length of a hook, not following curve, 0.038 mm. Shaft broad, and flat, but not bifid. Anterior (ventral) hooks articulate with a V-shaped transverse piece with expanded ends, and from point of the V two small prongs appear to articulate with the posterior hooks, but on this latter point there is some uncertainty. The disc itself is about as wide as the widest part of the body, with a rounded anterior margin, and rather straight posterior margin; and well set off from the caudal peduncle. The twelve marginal hooklets are grouped as in the preceding species, and have the same character.

The diameter of the pharynx is 0.017 mm. The intestine is rather short. The vagina is on the left margin, a little anterior to the middle, and leads into a small seminal receptacle crowded against the ovary. The testis is small, lying caudad of the ovary, with the vas deferens ascending on the left, dorsal to the vagina. A dilatation of the anterior coils of the vas deferens forms the seminal vesicle. The cirrus has a tubular base and is provided with two chitinous, twisted, terminal points. The path of the oviduct and its connections could not be made out.

The eyes are large, the anterior and posterior pairs about equi-distant.

This species was taken in multiple infestations from the gills of sunfishes from the reservoir of the fish hatchery at Constantia, along with *Cleidodiscus robustus* and a species described below.

Cotypes are in the collections of the Roosevelt Station.

Urocleidus, n. g.

Diagnosis.—Tetraonchinae, with intestine bifurcated but confluent posteriorly. Ovary and testes near center of body, vagina and seminal receptacle absent. Cirrus a single unbranched chitinous tube. Vitellaria from pharynx to posterior end of intestine. Attachment organ wedge shaped, with four large hooks of equal size connected by dorsal and ventral transverse pieces. Marginal hooklets 12 or 14 in number. Four eyes present. Type species: *Urocleidus aculeatus* (Van Cleave and Mueller).

This genus is related to the foregoing, but differs in the absence of the vagina, and the shape of the attachment organ. It differs from Empleurosoma, with which it has certain characters in common, in that the four large hooks of this latter genus are of unequal size, and only two small hooklets are present.

Urocleidus aculeatus (Van Cleave and Mueller, 1932)

Host.—*Stizostedion vitreum*, on gills.

This worm has been restudied, from whole mounts and sections, and although the material was not in good enough condition to allow interpretation of many points of detail, it was ascertained that the intestine is confluent posteriorly, whereas it was originally represented otherwise. A vagina seems to be absent. The caudal disc bears fourteen hooklets, as originally described.

These features are sufficient to remove this species from the genus Ancyrocephalus in which it was originally placed, since in Ancyrocephalus the intestinal limbs end blindly, and a vagina is present. It is therefore made the type of the new genus Urocleidus.

Urocleidus angularis n. sp.

Plate 47, Figures 12–16

Host.—*Fundulus diaphanus menona;* on gills.

This worm was studied from whole mounts, and on the basis of information at present available, may be placed in the above genus. Specimens vary from 0.260 mm. to 0.420 mm. in length, and are about 0.069 mm. to 0.075 mm. in width. The body form is tapering, and the disc set off from the rest of the body by a constricted caudal peduncle. The four large hooks lie in pairs, two on the dorsal and two on the ventral surface of the attachment organ, which is usually directed straight backwards. The large hooks have strongly curved exposed portions, and broad, flat, bifid proximal portions embedded in the disc. Each pair articulates with a chitinous transverse bar, the ventral one of which appears somewhat stouter and more curved than the dorsal. The largest dimension of a hook, not following the curve, is about 0.019 mm. The attachment organ is provided with 12 small hooks, with needle-like shafts, the inner ends of which are devoid of a knob or swelling. These lie partly dorsal, partly ventral, and partly lateral. Four eyes are present, but rather small, the anterior smaller than the posterior pair. The pharynx is 0.025 mm. in greatest diameter. No vagina could be found. The egg is roundly ellipsoidal, 0.05 mm. long by 0.033 mm. wide. The cirrus is a single, unbranched, long chitinous tube which pursues a spiral course before coming to its pointed extremity. The path of the oviduct or vas deferens could not be determined from the material in hand. In this species the anterior pair of eye spots very frequently seems to be fragmented into a scattered mass of pigment granules.

This species was found in small numbers on the gills of Fundulus from Oneida Lake. Cotypes are in the collections of the Roosevelt Station.

Urocleidus ferox n. sp.

Plate 47, Figures 7–9

Host.—*Eupomotis gibbosus;* on the gills.

This is a small species, an average individual measuring about 0.274 mm. long by 0.068 mm. wide. The attachment organ is well set off from the body by a sharp constriction of the caudal region, and is notable for its exceedingly large hooks. The four large hooks are approximately equal in size and shape, and are arranged in two pairs, one dorsal and one ventral. Each pair articulates with a chitinous transverse bar. The greatest length of one of the large hooks, not following the curve, is 0.070 mm. The large hooks have a very long exposed portion, which is rather straight for a distance and then bends sharply at a right angle near the point of the hook. The embedded portion is flat and bifid. There are twelve marginal hooks, so arranged that on each side a cluster of five radiate from a common center, with points projecting at equal intervals along the lateral edges of the disc. A pair of slightly larger hooklets are embedded deeply in the attachment organ, with bases in contact, and diverging toward the ventral surface, with their points on the ventral margin of the attachment organ. These 12 minor hooks have straight tubular bases, lacking any internal swelling. They all project toward the anterior end of the worm, and are much larger than the marginal hooklets of any other species described in this paper.

The eyes are four in number, the anterior smaller, and slightly closer together than the posterior. The pharynx is 0.021 mm. in diameter, and the intestine forks in the anterior region, but appears to be confluent behind. As far as could be determined from examination of whole mounts, a vagina is lacking. The vas deferens has a number of wide loops in the anterior region of the body. The cirrus is a long, single, unbranched, chitinous tube. Cotypes are in the collections of the Roosevelt Station.

Discussion

Of the large group of gyrodactyloid trematodes which Johnston and Tiegs (1922) described from Australian waters, these authors state that "all the new Australian forms described in this paper fall into new genera; indeed most of the species considered are so distinct from one another that they have had to be regarded as new generic types". It seems possible that the species above described represent more than the two new genera which have been created for their reception. Thus *Cleidodiscus fusiformis* and *C. oculatus* differ from *C. robustus* markedly in the arrangement of the large hooks of the caudal disc, and also in the character of the marginal hooklets. Furthermore, *oculatus* differs from *fusiformis* in lacking a constriction of the body. *Urocleidus aculeatus* differs from *U. angularis* and *U. ferox* in possessing 14 marginal hooklets. Whether there are further essential differences between *angularis* and *ferox* can not be answered until these species have been more thoroughly studied in detail. At least some of these differences appear to be of more than specific value. Notwithstanding these differences it appears wisest to follow a conservative course in the erection of genera until the native members of the group have become better known. Further studies upon the native gyrodactylids are under way, to include descriptions of additional species and further information on those already described.

Nematoda

Haplonema aditum n. sp.

Part III, Plate 39, Figures 1–4

Host.—*Anguilla rostrata.* In intestine.

Description: Females about 10 mm. to 12 mm. in length, 0.210 mm. greatest diameter. Esophagus about 1 mm. long, divided into two portions, similar in structure, but anterior narrower than posterior portion and slightly longer. Vulva at anterior margin of fourth quarter of body. Coils of ovary and uterus fill posterior two-thirds of body. Eggs rounded, shells fairly thin, about 0.06 mm. x 0.04 mm.

Males 8 mm. to 10 mm. long, tail sharply pointed posterior to anus. Spicules equal, 0.36 mm. in length. One large median pre-anal papilla, three pairs post-anal papillæ of which the first pair is frequently indistinct. A table has been prepared to show the differences that exist between the three species of Haplonema and on the basis of distinctions here set forth the specimens from the eel are described as *Haplonema aditum* n. sp.

Cotypes have been deposited in the collection of the U. S. National Museum, No. 32571.

Table No. 4. Comparison of Different Species of Haplonema

	H. immutatum	*H. hamulatum*	*H. aditum*
Size of female	15.0 mm.x 0.31 mm.	9.04 mm.x 0.16 mm	10 mm.–12 mm.x 0.21 mm.
Size of male	9.5 mm.x 0.2–0.18 mm	7.7 mm.–8.7 mm	8 mm.–10 mm..
Length esophagus	0.65 mm. in male 0.80 mm. in female	0.50 mm	1.0 mm.
Character esophagus	Evenly tapering, parts equal; 0.06 mm. anterior, 0.1 mm. posterior } diameter	Evenly tapering, parts equal; 0.02 mm. anterior, 0.06 mm. posterior } diameter	Abrupt change in diameter. Anterior part narrower and longer. 0.06 mm. anterior, 0.085 mm. posterior } diameter
Vulva	$\frac{5}{8}$ length from anterior tip	Somewhat posterior to that in *H. immutatum*	Anterior margin fourth quarter of body.
Eggs	Abundant, moderately thick shells, smooth; 0.065 mm.x 0.045 mm.	Not numerous, ovate or spherical, with pox on shell; 0.035 mm.x 0.055 mm.	Fairly numerous, thin smooth shells; 0.06 mm.x 0.04 mm.
Spicules	Equal, ribbon-like; 0.75 mm. long by 0.02 mm.	Equal. 0.12 mm. long, x 0.007 mm.	Equal, 0.036 mm. long
Papillae on tail of male	2 pairs pre-anal 3 pairs post-anal.	4 pairs pre-anal (?) 2 pairs post-anal (?)	1 large median pre-anal 3 prs. latero-ventral post-anal, 1st pair frequently indistinct. Occasionally two additional lateral pairs opposite 1st and 2nd post-anal papillae.
Papillae on tail of female	2 minute lateral papillae	(?)	None
Length cephalic alae	2.5 mm.– 3.0 mm	1.0 mm	1.75 mm.
Host	*Amia calva*	*Lota maculosa*	*Anguilla rostrata*

Baylis (1934) reports a nematode from the European eel, *Anguilla anguilla*, under the name *Paraquimperia tenerrima* (v. Linstow, 1878). Baylis made the new genus Paraquimperia to receive these worms, but this new genus is clearly a synonym of Haplonema, and so the form recorded by Baylis becomes *Haplonema tenerrima* (v. Linstow, 1878). It is possible that *H. aditum* from the American eel is a synonym of this species, but I have not compared specimens, and the point cannot be decided from the available figures. Both worms are approximately equal in size, and the character of the esophagus is in both cases similar.

Although they may be present, I have been unable to find in *H. aditum* the three pairs of preanal papillae which Baylis figures for *H. tenerrima*. The position of the vulva and the size of the eggs are similar in both species.

Eustrongylides sp.

Host.—*Fundulus diaphanus menona.* Immature worms encapsulated in mesenteries of host.

Three examples of this worm have been taken from Fundulus at the west end of the lake, near Shepherd's Point, during the early summer months of 1933. The worm is found coiled in a fibrous capsule about 1 cm. in diameter, attached to the mesenteries, lying in the body cavity. When taken from the capsule the worm is blood red, and about 10 cm. long. The body is of rather even diameter throughout, about 0.685 mm. The head is provided with the twelve papillæ, in two circles of six each, characteristic of the genus. The adult worm has not yet been discovered, and since there appears to be some uncertainty as to whether the species of this genus can be identified in the immature state, the form is not named here. A complete description with further data will appear elsewhere.

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(Additional references will be found at the end of Parts I, II, and III.)

THE ROOSEVELT WILD LIFE MEMORIAL

As a State Memorial

The State of New York is the trustee of this wild life Memorial to Theodore Roosevelt. The New York State College of Forestry at Syracuse is a State institution supported solely by State funds, and the Roosevelt Wild Life Forest Experiment Station is a part of this institution. The Trustees are State officials. A legislative mandate instructed them as follows:

"To establish and conduct an experimental station to be known as 'Roosevelt Wild Life Forest Experiment Station,' in which there shall be maintained records of the results of the experiments and investigations made and research work accomplished; also a library of works, publications, papers and data having to do with wild life, together with means for practical illustration and demonstration, which library shall, at all reasonable hours, be open to the public." [Laws of New York, chapter 536. Became a law May 10, 1919.]

As a General Memorial

While this Memorial Station was founded by New York State, its functions are not limited solely to the State. The Trustees are further authorized to cooperate with other agencies, so that the work is by no means limited to the boundaries of the State or by State funds. Provision for this has been made by the law as follows:

"To enter into any contract necessary or appropriate for carrying out any of the purposes or objects of the College, including such as shall involve cooperation with any person, corporation or association or any department of the government of the State of New York or of the United States in laboratory, experimental, investigative or research work, and the acceptance from such person, corporation, association, or department of the State or Federal government of gifts or contributions of money, expert service, labor, materials, apparatus, appliances or other property in connection therewith." [Laws of New York, chapter 42. Became a law March 7, 1918.]

By these laws the Empire State has made provision to conduct forest wild life research upon a comprehensive basis, and on a plan as broad as that approved by Theodore Roosevelt himself.


ONEIDA LAKE
Belknaps Landing
BIG BAY
Dry Land Pt
Deer Pt
Willow Pt
Paddyfoot Pt
Paddyfoot Bay
Fairchild Pt
Shaw Pt
Shaw Bay
Fairchild Bay
Johnson Bay
Nannyberry Pt
Phillips Pt
Three Mile Bay
Sand Pt
Baker Pt
Baker Bay
Bullhead Bay
CONSTANTIA
LITTLE ISL
LONG ISL
WANTRY ISL
Mathews Pt
Durkin Bay
Taft Pt
Taft Bay
Bernhard Bay
Dixon Pt
Potter Bay
Wehe Bay
CLEVELAND
Colton Bay
Godfrey Pt
Eaton Bay
WEST VIENNA
NORTH BAY
SYLVAN BEACH
SOUTH BAY
Lewis Pt
Messenger Bay
Chapman Pt
Bushnell Pt
LAKEPORT BAY
LAKEPORT
LEETE or DUTCHMANS ISLAND
Shackelton Pt
Billington Bay
Damon Pt
Archer Bay
Hitchcock Pt
BRIDGEPORT
Maple Bay
Graves Bay
LOWER SOUTH BAY
Short Pt
Short Point Bay
Long Point
Ladd Pt
Walnut Point
Fiegel Pt
Muskrat Bay
Shepard Pt
BREWERTON
Wilson Pt
FRENCHMAN ISLAND
DUNHAM ISLAND
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LEGEND —
-6 ft contours
-12 ft contours
SCALE IN MILES —
0 ¼ ½ ¾ 1 2 3 4

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